DIEBACK OF RURAL EUCALYPTS: DIETARY QUALITY OF FOLIAGE AND INSECT HERBIVORY

by

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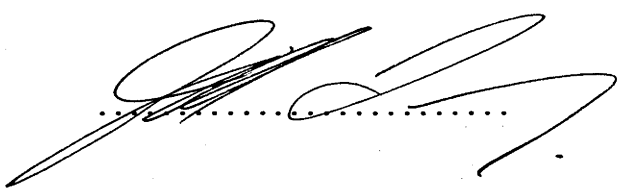
STATEMENT

The work presented in this thesis is my own. Specific contributions by others have been referred to in the text and acknowledgements.



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At the risk of repeating myself, I would like to again thank my principal supervisor, Dr Ian Noble, and the other members of my supervisory committee, Dr Phil Carne, Dr Cliff Ohmart and Professor Tom White, for their support and guidance throughout the study. My colleagues in the Department of Environmental Biology were always friendly and supportive; I would particularly like to thank Dr Bruce Wellington and Ms Helen Armstrong for many stimulating discussions. Generous and reliable technical assistance made the study possible; for this I would particularly like to thank Mr Peter Cochrane, Ms Sue Wood, and Ms Susan Allen. In addition Ms Jane Vickers and Ms Leonie Hoorweg provided much advice and assistance about word processing.

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ABSTRACT

Dieback of native trees on farms in Australia - rural tree dieback - is often associated with chronic defoliation by insects. Where this association occurs, trees with severe dieback are commonly found growing adjacent to healthy trees which appear, in other respects, to be very similar to the trees with dieback. I investigated possible reasons for this variation in susceptibility for Eucalyptus blakelyi, a common species of eucalypt on pastoral lands in the southern tablelands of south eastern Australia.

The values I obtained when assessing the extent of insect damage to foliage were very dependent on the technique of assessment. For example, when I compared several commonly used techniques I found a ten-fold difference between the highest and lowest values I calculated for samples from the same trees.

Dieback-affected E. blakelyi trees were more heavily grazed by insects than were healthy trees growing nearby. The foliage from the dieback trees tended to be younger, which contributed to its greater susceptibility to insect grazing, but foliage from dieback trees was also damaged to a greater extent than foliage of similar age from healthy trees.

Dieback trees' foliage also tended to be nutritionally superior for insects, compared with healthy trees' foliage. Some of the differences in dietary quality reflected differences in the average age of the foliage of healthy and dieback trees. But when statistical models were used to equalize the effects of differences in tree phenology, leaves on dieback trees still tended to contain more water and nitrogen, and to be rounder and to have lower specific weights. Many of the dietary quality variables were correlated with each other. This is probably why multiple regression equations incorporating seasonal means of several quality variables were grossly different between years, although they explained a high proportion of the variance in seasonal herbivory.

In a series of glasshouse experiments, I investigated whether differences in the nutritional quality of foliage were genetically determined, or caused by environmental stress. Using seedlings and

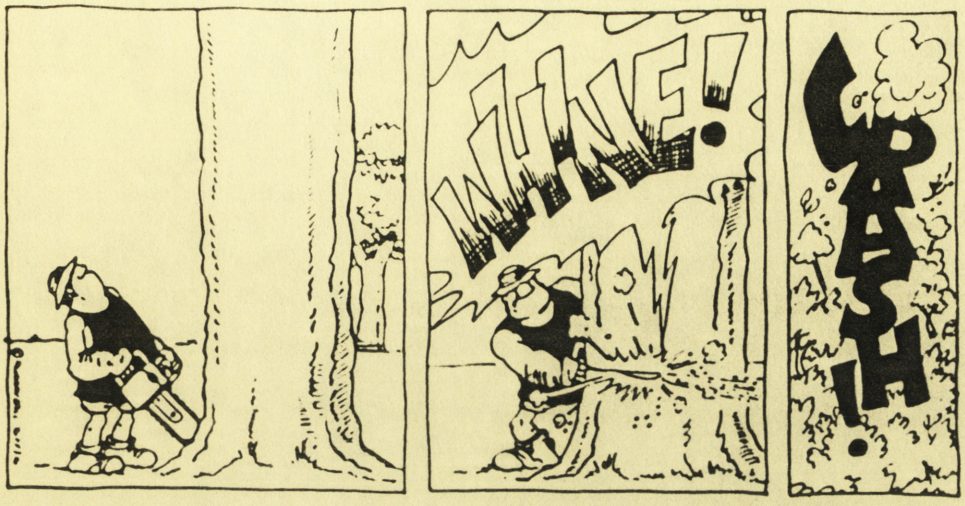
grafted plants derived from dieback and healthy populations of trees, I tested the influence of: depletion of nutrients, addition of excess phosphate, drought, waterlogging, and saline waterlogging on the nutritional quality of foliage. Differences in the foliar properties of plants from different genetic sources were not consistent with the differences between the source populations. Most of the environmental stresses applied caused a reduction in foliar quality, (decreased water and nitrogen contents, and increased specific leaf weights). I hypothesize that the enhanced nutritional quality of the foliage of dieback-affected trees is more likely to be a consequence of benign growing conditions (e.g. improved soil fertility), than of environmental stress. Field data for soil properties and the effect of drought on mature trees are consistent with this view.

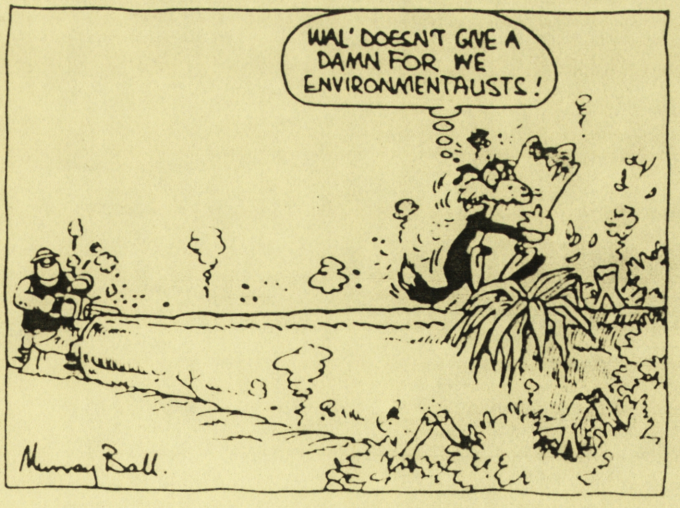
I attempted to test whether seedlings grown under a favourable nutrient regime would be more damaged by insects, in a field experiment in which seedlings were grown in boxes placed on platforms in the canopies of mature trees. Unfortunately common brushtail possums (Trichosurus vulpecula) severely damaged many of the seedlings before I could measure insect damage. (The possums selectively browsed on nutrient-rich seedlings. Limited data suggest that the animals may have selected for foliage with a high concentration of sugar and a low concentration of tannin.)

Defoliation appears to enhance the susceptibility of regrowth foliage to damage by insects. The foliage that regrew on three mature trees that I had artificially defoliated was nutritionally superior to the foliage it replaced, and was much more heavily damaged by grazing insects. There was a transient increase in the tannin content of the regrowth foliage, but this was apparently ineffective in defending it from subsequent herbivory. The dietary quality of the regrowth foliage was more similar to that of the foliage on dieback, rather than the healthy trees. Therefore I suspect that the enhanced nutritional quality of the foliage of dieback trees may be maintained, in part at least, by a feedback between repeated cycles of defoliation by insects and compensatory growth by trees.

This thesis is written as a series of manuscripts, all of which have been submitted to journals for publication.

CONTENTS





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INTRODUCTION

The research reported in this thesis was inspired by an interest in rural tree dieback, a disease syndrome affecting many native trees on Australian farms. Public awareness of the problem is high, but has not been matched by research activity. Details of the distribution and severity of rural dieback are documented for only a few localities, and even within these localities the cause of the dieback is seldom known with any certainty. However, defoliation by insects is often implicated, and it is on this aspect that I have concentrated my research effort. Specifically, I have investigated reasons for intraspecific variation in the susceptibility of trees to insect grazing, in the context of rural tree dieback.

The thesis is presented as a series of manuscripts that have been submitted for publication. The publication status of each is indicated on its title page. Their format has been standardized, for ease of reading, and I have presented a single list of all the references cited, to minimize repetition. I am the sole author of all but the first manuscript, though I am very grateful for the assistance which I received and have acknowledged in the others. The first manuscript was prepared jointly with Mr F.R. Wylie, of the Queensland Department of Forestry, for a poster I presented at a conference in September, 1985. Mr Wylie and I worked together closely during my honours studies at the University of Queensland, and we have both pursued our research interests in rural tree dieback at a postgraduate level. The poster presentation was a synopsis of our hypotheses about the interactions that may be involved in rural dieback. I prepared the text and the manuscript, using the results of a survey conducted by Mr Wylie. We prepared the conceptual model together.

I have used this conceptual model to link the sections of my thesis. Each section is concerned with a specific question arising from a particular interaction, or set of interactions, postulated in the model. This question, and its context within the framework of the conceptual model, precedes each section. Its answer, and the relevance this has to the model, puts each section back into perspective. I discuss the implications of these answers for future research into both rural tree dieback and insect/host plant dynamics in the conclusion to the thesis.

THE IMPACT OF TREE DECLINE ON REMNANT WOODLOTS ON FARMS

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Tree decline in rural areas, and the associated hazards of soil erosion and salinity, are among the foremost conservation issues in Australia. About 30% of Australia's forests and woodlands have been cleared or severely modified since European settlement (Wells et al. 1984). Since the late 1960's and early 1970's there has been a marked increase in the rate of decline of remnant native vegetation on farmland in many parts of Australia. Tree loss in rural areas involves three elements. The first is the deliberate removal of trees as part of farm management. The second is the death of trees due to old age, coupled with a paucity of recruitment of tree seedlings because of active suppression, grazing, and competition with improved pastures. The third element - rural dieback - is the premature and relatively rapid decline and death of native trees on farms, apparently as a consequence of interacting environmental stresses. Rural dieback affects many different species of trees, of all ages, in most states (Old et al. 1981).

A number of features characterise 'healthy' remnants of native woodland. These remnants are usually substantial (several hectares or more) and have been minimally disturbed by man or grazing livestock. There is a high degree of diversity: in vegetation structure, in plant and animal species present and in the age classes of trees and shrubs represented. In such remnants, insect grazing pressure on trees is generally light to moderate. Most trees have normal, full-leaved crowns with very few dead or leafless branches and little obvious epicormic growth. Only the occasional tree shows symptoms of disorder and there are relatively few dead trees.

In contrast, remnant woodlots with dieback are usually small and have been severely disturbed. They lack diversity of vegetation structure, floristics, age classes and fauna. In such woodlots, the pressure on trees from grazing by insects is usually severe and sustained. Many trees have sparse crowns with some death of both minor and major branches and a high proportion of epicormic growth. Tree disorder is widespread and tree death common.

Research in Queensland (Wylie & Johnston 1984) has shown a direct relationship between the extent of modification of original tree cover and the severity of rural dieback. Deliberate tree clearing, and the intensification of land use associated with it, are pivotal factors in the development of rural dieback.

Remnant woodlots on farms represent ecosystems which are precariously balanced. Once a dieback sequence is initiated, positive feedback can cause an originally stable woodlot to rapidly regress through a series of unstable states to treeless grassland (Fig.1). Small or highly modified woodlots have least buffering capacity and are therefore most at risk. In the long term both smaller woodlots and woodlots which have been structurally or floristically modified have little chance of survival unless supplemented by replanting or by natural regeneration. As land use intensifies dieback will accelerate, and will continue to erode the value of remnants of native woodlands on farms as a conservation resource, unless there is positive intervention to restore ecosystem comlexity. Research to establish the parameters which define a stable woodland remnant is urgently needed.

Rural tree decline has major consequences for conservation of biota, soil and water, at a scale which affects both rural and urban communities. Successful maintenance and rehabilitation of existing farm woodlots, and the establishment of new ones, require an understanding of the dynamics of rural dieback, if its spread is to be arrested and its resurgence prevented.

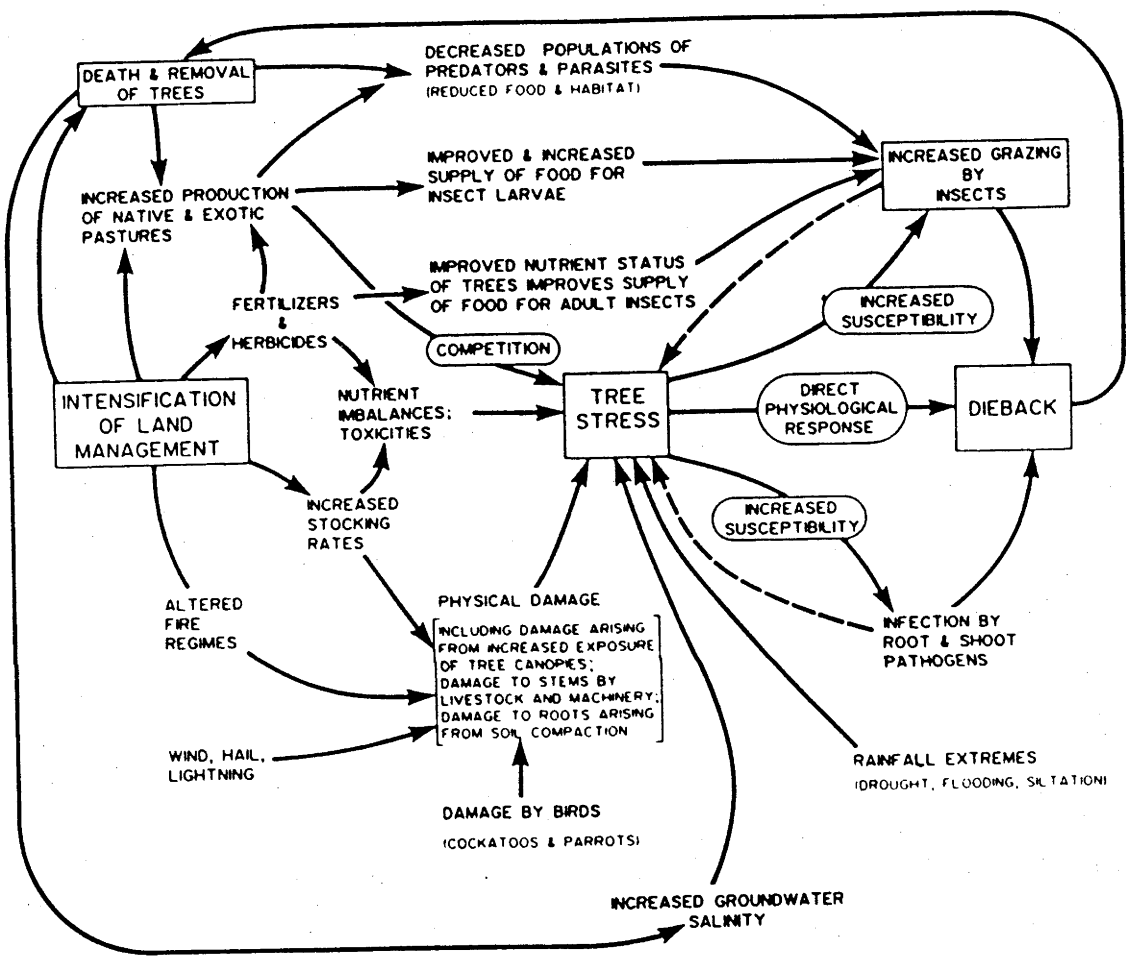
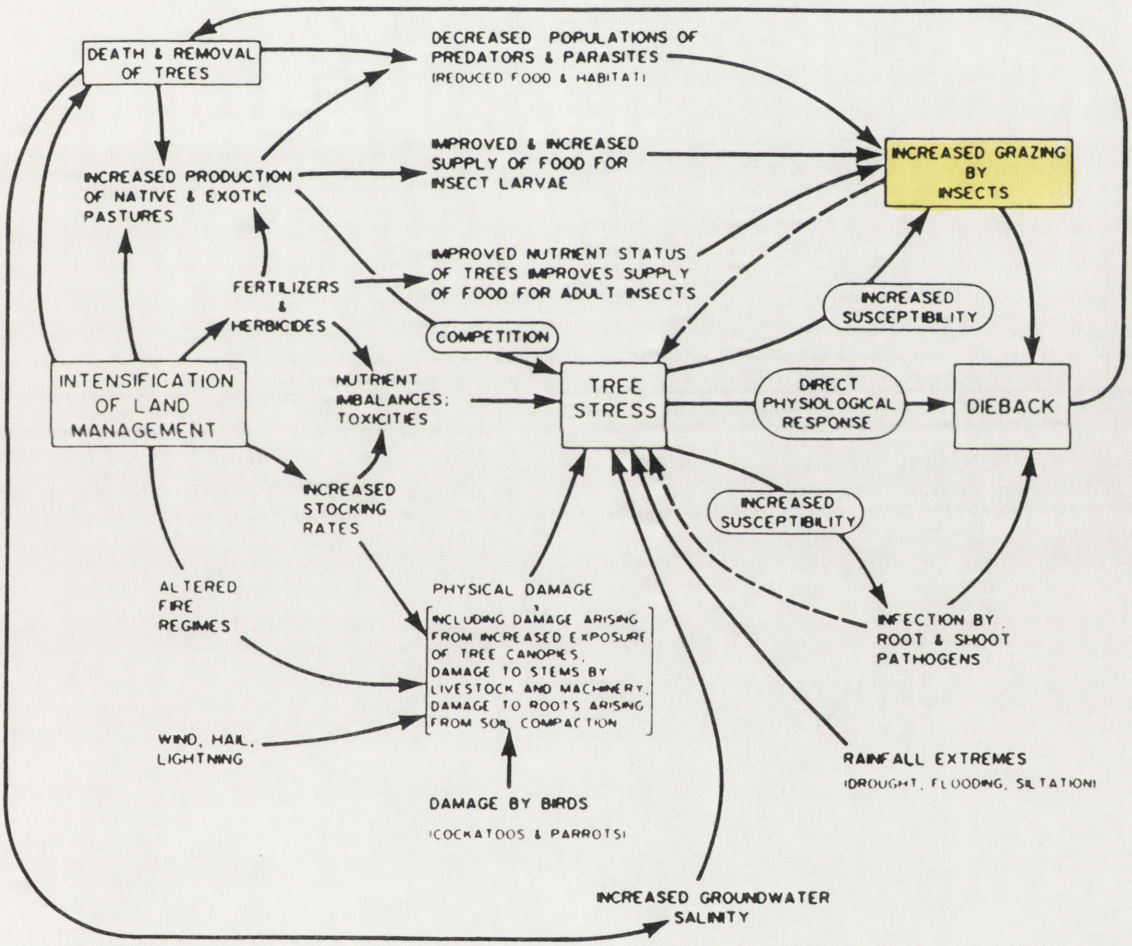


Figure 1. A conceptual model of the development of rural dieback.

Do trees with dieback experience more damage than healthy trees from grazing by insects?



A COMPARISON OF METHODS OF ASSESSING INSECT DAMAGE TO FOLIAGE OF EUCALYPT TREES

AUTHOR: JILL LANDSBERG

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ABSTRACT

I compared, at several scales of resolution, the most commonly used methods of assessing the extent of damage that grazing insects cause to eucalypt foliage.

1. For individual leaves I compared measuring the area of damage on a digitizer with assigning leaves to ordinal damage classes following visual inspection. Operators overestimated the values of the midpoints of the damage classes, and these estimates were operator-dependent. However both methods achieved similar results when the midpoints of ordinal damage classes were calibrated for each operator from digitizer measurements.
2. Leaf damage is usually expressed as a proportion of the total potential leaf area. In my study this value changed during leaf expansion. I made holes in young leaves that continued to expand after being damaged; the holes did not expand as quickly as did the leaves and the proportion of leaf area represented by the damage therefore decreased.
3. When I calculated annual herbivory losses from tree canopies using different methods for the same sample of leaves there was a ten-fold difference between the highest and lowest values I obtained. Discrepancies arose because: a) It was difficult to determine the fate of tagged leaves which were lost in the interval between measurements. b) The actual damage incurred during the year of the study was only about half the damage the leaves had accumulated during their life spans. c) Damage expressed as a mean proportion of each leaf damaged underestimated the mean proportional area of the sample of foliage that was actually damaged. This was because the frequency distributions of damage incurred by individual leaves in each tree's sample were heavily skewed; small leaves were damaged more than large ones, and many leaves were damaged a little while few were damaged a lot.
4. Annual herbivory losses estimated from leaves cut from trees at discrete intervals (discrete sampling) were higher than those estimated on samples of leaves monitored on tagged shoots (longterm sampling); discrete sampling was more economical of time but yielded less information about canopy dynamics.
5. Trees that were grazed heavily could be successfully discriminated from trees that were lightly grazed by visual assessment of the appearance of their canopies.

INTRODUCTION

The controversy which exists regarding the extent to which the canopies of eucalypts are grazed by insects results, at least in part, from the difficulty of comparing data collected using very different techniques (Ohmart 1984). Lowman (1984, 1985) has indicated that a similar difficulty exists with comparing data on herbivory from rainforest canopies.

In some studies insect damage is visually assessed for whole canopies, which are assigned to different damage categories. This is usually used when insect populations have reached pest proportions (e.g. Carne et al. 1974), or for insects which completely defoliate sections of canopies (e.g. Carne 1965).

However, most studies of herbivory on eucalypts have relied on assessing damage to a sample of leaves drawn from the canopy. During her studies of rainforest canopies, Lowman (1984, 1985) described two different methods of sampling leaves for such assessment, which she termed 'discrete' and 'longterm'. Longterm sampling, whereby leaves were permanently marked and herbivory was measured over a time period, gave higher estimates of grazing damage than did discrete sampling, where leaves were cut from the canopy and damage was assessed on the collected leaves. This was because longterm sampling enabled leaves which were totally eaten by herbivores to be included in the assessment. Caution is required, however, in distinguishing losses of whole leaves as a result of insect damage from other causes of leaf shed such as natural senescence, wind abrasion and desiccation. These other causes can account for substantial loss of leaves. Pook (1984a) attributed the loss of some 49% of immature E. maculata leaves to such causes, since insect browsing was slight in the canopies he studied.

Longterm sampling has the advantage that each incident of damage is included only once in the calculation of annual losses from herbivory. If discrete sampling is used for trees such as eucalypts, which retain their leaves for three or more years (Jacobs 1955; Pook 1984a), difficulties arise in interpreting results on an annual basis. If damage is instead expressed as loss of current season's foliage, recent damage to previous season's foliage is neglected. Also,

expressing damage in terms of current season's growth has little value if foliage can be produced in all months of the year under favourable conditions, a pattern common to many eucalypts (Pook 1984a; Specht & Brouwer 1975). Further problems arise if damage is simply averaged over all ages of leaves present in the canopy and includes damage incurred in previous growing seasons. Average levels of herbivory will then depend, amongst other things, on the life span of leaves.

Despite these problems, most leaf-based assessments of levels of insect grazing on eucalypts have been made on leaves which were cut from canopies at discrete times (e.g. Burdon & Chilvers 1974; Fox & Morrow 1983; Journet 1981; Kile 1974; Landsberg & Wylie 1983; Ohmart et al. 1983a, b, 1984; Specht & Brouwer 1975). Pook's studies of the canopy dynamics of E. maculata canopies (1984a, b, 1985) are the only exception, though they were not designed to study herbivory and he noted very little insect grazing.

The extent of insect damage to foliage sampled discretely or on a longterm basis, is commonly assessed by either of two methods. The actual area of leaves may be measured using an area measuring instrument, and compared with the area that the leaves might have been (or grown to) in the absence of damage (e.g. Burdon & Chilvers 1974; Journet 1981; Kile 1974; Ohmart et al. 1983a, b, 1984). Alternatively, a visual estimate is made of the proportion of each leaf missing, and leaves are assigned to damage categories such as 0%, <1%, <10%, <25%, <50%, <75%, and <100% (e.g. Fox & Morrow 1983; Landsberg & Wylie 1983).

The results obtained from either method are always expressed as a proportion of the total area of foliage in a sample. This allows comparisons to be made between leaf cohorts, between trees, and between species, regardless of variations in leaf sizes (although these comparisons are only valid if they relate to data collected in the same way), but gives only limited information on the amount of leaf material consumed by herbivores, or lost from trees. Lowman (1984, 1985) discusses these limitations in some detail. Not only does the size (area and specific weight) of fully expanded leaves vary, but young leaves (and their contained holes) may continue to expand after they have been damaged.

In this study I compared estimates of insect grazing in the canopies of Eucalyptus blakelyi Maiden trees growing in remnant woodland in the Australian Capital Territory. I rated the condition of the canopies of a number of trees, and measured levels of damage on samples of leaves from their canopies. I compared two methods of assessing the extent to which individual leaves were damaged; visual estimation of the proportion of each leaf missing, and instrumented measurement of actual and extrapolated potential leaf areas. I also compared two different ways of sampling leaf populations. Damage was assessed at regular intervals for a year on leaves cut from canopies (discrete sampling), and on tagged leaves which remained in the canopies until removed by natural agencies (longterm sampling). In a separate experiment the relationship between the sizes of holes, and the proportion of leaf area they represented both before and after leaf expansion had occurred, was investigated for several ages and shapes of leaves.

METHODS

STUDY SITES AND TREES

Measurements for this study (apart from those for the 'growing holes' experiment) were made from October 1982 to October 1983 on mature E. blakelyi trees growing on a grazing property at Hall, in the ACT. The site consists of a semi-cleared remnant of native woodland on a gentle hillslope with some rock outcrop; the pasture is dominated by Phalaris sp. and managed for grazing of sheep and cattle. E. blakelyi is the dominant tree species. The canopies of trees at the site varied from apparently healthy, to showing marked dieback. Since the dieback was presumed to relate, at least in part, to severe insect grazing, the sample of trees was chosen to include equal numbers of 'dieback' and 'healthy' trees.

CANOPY ASSESSMENT

The condition of the trees' canopies was assessed from four crown characteristics, with scores allocated according to a modification of a forestry rating scheme in which a tree score was correlated with rate of diameter increment (Grimes 1978). Scores for crown size ranged from 5 (wide, deep, roughly circular) to 1 (no true crown); for crown density from 9 (very dense leaf clumps evenly distributed over crown) to 1 (very few leaves anywhere in crown); for dead branches from 5 (no visible branch death) to 0.5 (crown dead, only main stem alive); and for epicormic growth from 3 (growth concentrated at extremities of branches) to 0.5 (growth concentrated on epicormic shoots along main stem).

ASSESSMENT OF DAMAGE ON INDIVIDUAL LEAVES

There were three objectives of these measurements. The first was to test the assumption that midpoints of damage categories are an accurate representation of the average damage sustained by the leaves assigned to these categories. The second was to test whether the the values obtained for mean proportion of foliage damaged per tree were comparable when calculated from both visual assessment and from instrumented measurements. The third was to test the consistency of visual estimations made by different operators, and by the same operator at different times. (Eucalypt leaves sustain a variety of types of damage as a result of insect feeding, including skeletonizing, distortion and necrosis in addition to removal (Landsberg & Wylie 1983), but only removal was assessed in this study, and by 'damage' as used here I mean only complete removal of pieces of leaves.)

Routine procedure for visually estimating mean proportion of foliage damaged per tree usually involves an operator assessing a sample of leaves from a tree and scoring the number of leaves which he or she assigns to each of a number of damage categories. The mean damage is then calculated as $\Sigma fx/\Sigma f$, where f is the number of leaves in a category, and x is the midpoint of that category. I used the following damage categories (nominal category midpoints are shown in

parentheses): 'no damage' (0%), 'a little damage' (1%), 'about an eighth damaged' (12.5%), 'about a quarter damaged' (25%), 'about a half damaged' (50%), 'about three quarters damaged' (75%), and 'most of the leaf damaged' (99%).

To test the accuracy of these nominal category midpoints, I collected 500 leaves from 10 E. blakelyi trees at the study site, to include a range of leaf sizes, shapes, and degrees of damage. These were first assigned to damage categories, then the percentage of each leaf damaged was measured on a digitising board (Ohmart & Stewart 1985). Leaves were placed on the digitising board under a thin sheet of perspex, and the estimated original leaf outline was drawn onto the perspex. Percentage of each leaf damaged was then calculated from the ratio of the area of leaf missing to the extrapolated original outline area, on a desk top microcomputer connected to the board. From these values the mean % damage per leaf represented by each category was calculated.

Two operators (JL and SA) each performed this operation on the same batch of 500 leaves, to test between-operator consistency.

To compare the values obtained from the two methods for the proportional area of damage on foliar samples, samples were collected from nine trees. These consisted of three healthy trees with adult-form, lanceolate leaves, three trees which had been artificially defoliated the previous year and had juvenile-form, ovate leaves, and three trees with dieback, whose leaves were intermediate in form. Most of the leaves collected (at least 50 per tree) were mature, and had developed in the current growing season. The sample from one of the healthy trees also included some 20 older leaves which dated from the previous growing season, and these were treated as a separate subsample. The proportional area of damage on each sample was calculated from both visual estimation and digitizer measurements. Both operators made the visual estimations independently, and one (SA) repeated her estimations several months later, to test the reproducibility of the estimations.

'GROWING HOLES' - THE RATE OF EXPANSION OF HOLES MADE IN YOUNG LEAVES AS BOTH LEAVES AND HOLES EXPAND

This experiment was conducted on E. blakelyi trees growing on the campus of the Australian National University. Holes of known area were punched in young, partially expanded leaves whose outline area had been measured using a portable area meter. The holes were punched on the midvein of the leaves and did not break the leaf margins. (Midveins could not be avoided on the narrower leaves, so for consistency all leaves were treated similarly.) Measurements of both the area occupied by the hole and the area of the leaf outline (extrapolated if necessary) were repeated after the leaves ceased expanding. Three holes were cut in three leaves of different ages on each of three branches of five seedling, five sapling and five adult trees (405 holes in 135 leaves on 15 trees) (Table 1). The data were analyzed using analysis of variance and generalized linear modelling subroutines from the GENSTAT computer program (Alvey et al. 1982).

LONGTERM SAMPLING OF LEAVES

Longterm samples were monitored on two 'healthy' and two 'dieback' trees at about fortnightly intervals during the growing season (from October 1982 to March 1983) and monthly thereafter, for a year (till September 1983). Time constraints limited the number of trees which could be monitored, since recording changes in the leaf samples took from two to six hours for each tree.

A further limitation was imposed by access to the tree canopies, which was gained via poles (one positioned near each tree), fitted with climbing spikes. In order to determine where to position the poles, a pilot study was conducted on three other trees at the site to investigate the distribution of herbivory within the canopies. Differences between canopy positions were not significant ($F<1$; $df=1,8$; $P0>0.1$), probably because the sample size was small. However there was a consistent trend for damage to be greater in the lower canopy (9.8 ± 2.3 % compared with 8.4 ± 2.3 % in the upper canopy), and on the north side (9.5 ± 2.3 %) compared with the south (9.0 ± 2.3

%). Similar differences have also been reported from other studies (Lowman 1985; White 1970). Thus to maximize the likelihood of the sampled branches sustaining insect damage, the poles were positioned on the northern side of each tree. Each pole was fitted with a platform which projected into the upper canopy, and increased access to different branches.

Ten terminal branchlets were tagged in the upper and lower canopies of each tree. Choice of branchlets was constrained by access, but wherever possible branchlets originating from different major branches were chosen. Each branchlet initially supported about five leaves distal to the tag, and these leaves constituted the initial sample (about 100 leaves per tree). Tracings were made of all leaves in the sample, and changes to leaves were recorded on these tracings on subsequent sampling occasions. Any new leaves which were initiated distal to the tag were included in subsequent samples. This, together with leaf abscission, resulted in patchy distributions of leaf samples within the canopies by the end of the study. Actual and estimated potential leaf areas were measured on a digitising board, as described previously.

DISCRETE SAMPLING OF LEAVES

Discrete samples were collected, using pole pruners, from another five 'healthy' and five 'dieback' trees in the same stand, to coincide with measurements of long term samples. Each sample comprised about 100 leaves growing on four branches cut from upper and lower canopy positions on the north and south sides. Each branch supported about five branchlets which usually carried about five leaves each. A maximum of 50 leaves were assessed for each subsample. This usually necessitated further subsampling, which was done by choosing every second or third leaf on each stem. The proportion of each leaf missing was estimated visually for each subsample, as described above.

RESULTS AND DISCUSSION

CANOPY ASSESSMENT

Dieback trees had more dead branches, more epicormic foliage and less dense canopies than did healthy trees. Their assessment ratings were significantly different ($t=6.9$; $df=12$; $P<0.01$); dieback trees had a mean score of 9.7 and healthy trees had a mean score of 16.4. Leaves of dieback trees were also significantly more damaged by insects ($t=2.31$; $df=12$; $P<0.05$). The mean proportional area of damage on samples from dieback trees was 18.5%, compared with 13.3% for healthy trees.

ASSESSMENT OF DAMAGE ON INDIVIDUAL LEAVES

Nominal midpoints of the damage categories were always greater than the measured values of average percentage of area missing from each leaf assigned to that category (Table 2). Thus each operator tended to overestimate the proportion of each leaf that was damaged. In addition, the extent of overestimation was significantly different between operators for the higher categories of damage (t tests; $P<0.05$).

When calibrated, rather than nominal, category midpoints were used to calculate mean leaf damage of the canopy samples, they yielded results which were in good agreement with values measured on the digitizer (Table 3). (Calibrated midpoints were the values measured for each operator of the mean damage per leaf assigned to each category.) Regressions of the estimated values (E) against the measured values (M) were highly significant, with coefficients close to unity. Repeat estimations of the same samples (SA1 and SA2) also gave a highly significant regression.

For SA: $E = 1.07\ M$ ($r^2=.99$, $P<0.01$)

For JL: $E = 1.14\ M$ ($r^2=.96$, $P<0.01$)

For the repeats: $SA1 = 1.01\ SA2$ ($r^2=.99$, $P<0.01$).

These results show that when they are calibrated, the results of visual estimations agree well with values measured on a digitizer, and are also highly consistent between operators and over time.

'GROWING HOLES'

I tested how well additive and multiplicative generalized linear models fitted the data from this experiment. If an additive model is most appropriate then the change in the area of a hole as it grows is some additive function of the change in area of the leaf in which it was made. I tested:

$$HA2\ (-HA1) = \mu + \mu_f + \beta_2 LA2 - \beta_1 LA1 \qquad \ldots 1a, \text{ or}$$

$$HA2\ (-HA1) = \mu + \mu_f + \beta(LA2 - LA1) \qquad \ldots 1b$$

where HA2, the dependent variable, is the area of a hole when the leaf is fully expanded, and HA1 is the initial area of the hole. (Since it was constant in this experiment ($0.27cm^2$), it was not included in the statistical fitting of the models, though it was used in the derivation of the final model.) μ is a parameter constant, and μ_f is a parameter constant associated with the factors included in the experimental design. β_2 and β_1 are parameter constants associated with rates of change of the independent variables, expanded leaf area (LA2) and initial leaf area (LA1). If these are equal $\beta_2 = \beta_1 = \beta$ (equation 1b).

If a multiplicative is more appropriate then the relationship between the area of a leaf and its contained hole is logarithmic. I tested:

$$\ln HA2\ (-\ln HA1) = \ln(HA2/HA1) = \mu + \mu_f + \beta_2 \ln LA2 - \beta_1 \ln LA1 \quad \ldots 2a$$

$$\ln HA2\ (-\ln HA1) = \ln(HA2/HA1) = \mu + \mu_f + \beta \ln(LA2/LA1) \quad \ldots 2b$$

The three factors included in the experimental design (tree age, leaf age, and hole position; Table 1) did not contribute equally to changes in the areas of holes and leaves. Observations during the experiment showed that some holes and leaves became very distorted as the leaves grew. This was especially true of holes made in the tips of leaves. The margin of these holes often coalesced with the margin of the leaf, and sometimes caused loss of the whole leaf tip, so that the potential area of such leaves could only be estimated. Leaf age also had a variable effect, with the holes made in the youngest leaves causing most distortion of leaf and hole. No such differences were associated with the age of the trees.

Thus for the first series of models tested, the fitting was repeated for each level of leaf age and hole position, and tree age was used as a term (equivalent to μ_f in equations 1 and 2). Nine additive and nine multiplicative models were tested. To examine whether the leaf area coefficients (β_1 & β_2) could be regarded as equal, the models were fitted both with LA1 and LA2 (or lnLA1 and lnLA2) as separate terms and also with the change in leaf area (LA2-LA1) or (lnLA2-lnLA1) as a single term. The significance of differences between models incorporating different terms was tested from the F statistic (F= change in residual sums of squares between the models tested divided by the smallest residual mean square).

Tree age significantly improved the fit of only three of the 18 models tested, and none of these three explained more than 20% of the total variance. In only one of the models, the additive model for nearly mature leaves with holes at their bases, was there a significant difference ($P<0.10$) between fitting LA1 and LA2 separately compared with fitting (LA2-LA1) as a single term. The additive models tended to explain more of the variance (least was 17%, most was 73%) than did the multiplicative models (least was 11%, most was 58%). However in residual plots from the additive models the residuals tended to become more scattered as the fitted values increased,

indicative of non-constancy of error variance. In contrast, the residual plots from the multiplicative models tended toward more random scatter, suggesting that they may, in fact, be more appropriate, despite their slightly poorer level of explanation. Residual plots also indicated the presence of four outlying values, which were excluded from the next stage of the analysis.

A comparison of the coefficients associated with the change in leaf areas (β) for each of the models (table 4 & 5), showed that the models for holes in the tip position differed markedly from the others. This was expected, since the degree of distortion caused by the tip holes had already been noted. The coefficients for the other two hole positions were very similar for both the additive and the multiplicative models, and were also very similar for all ages of leaves in the multiplicative models, but not for the additive models. This suggested that, while leaf age was a significant factor in the additive models, this effect was much reduced in the multiplicative models.

The second series of models I tested followed from these results. Both an additive model and a multiplicative model were run on the combined data set, from which were excluded the values for holes in leaf tips and the outliers. Tree age was not included as a factor, but leaf age was, as was a term for the interaction between leaf age and the change in leaf area. Again, terms for both the change in leaf area and for each leaf area separately were tested.

The final models presented (tables 6 & 7) include only those terms whose addition significantly improved the models' fit (F tests, $P<0.10$). Although the additive model explained slightly more of the variance, the multiplicative model was deemed most appropriate for two main reasons. Firstly it was parsimonious, in marked contrast to the additive model which included coefficients for the initial and final leaf areas, for leaf age, and for the interaction between leaf age and fully expanded leaf area. Secondly, the residual plot from the additive model indicated non-constancy of error variance; the multiplicative model did not suffer from this problem. Thus the model which best described the relationship between growing leaves and holes in this experiment was:

$\ln HA2 = -1.29 + .76 \ln(LA2/LA1)$ (Table 7).

This model can be made more generally applicable if the area of the initial hole used in this experiment ($HA1 = 0.27cm^2$) is incorporated. Then the model becomes:

$\ln(HA2/HA1) = -1.29 + .76 \ln(LA2/LA1) - \ln(HA1)$; i.e.

$HA2/HA1 = (LA2/LA1)^{.76}$ ...3

The exponent of the constant term is unity, an important feature of this model and a partial validation of it, since it successfully predicts that holes will cease expanding when leaves do (i.e. when LA2 = LA1 then HA2 = HA1). Other models of the rate of hole expansion do not always achieve this prediction.

This model contrasts with the usual assumption that holes and leaves expand at the same rate. Reichle et al. (1973) and Lowman (1982) conducted similar experiments with leaves from different tree species. However, both studies were based on relatively small sample sizes. Lowman measured 15-25 leaves for each of five tree species, and derived different regressions for each. The final graph illustrating Reichle et al.'s experiment (Fig.6, p1084, Reichle et al. 1973) shows only 10 points. In addition, in neither study were the areas of the fully expanded leaves actually measured. Lowman derived relationships between the change in hole area and the change in leaf length, rather than leaf area. Reichle et al. measured expanded leaf length and width, and calculated 'gross leaf area' from this, from a regression equation. The regression they derived for the relationship between the change in leaf area and hole area was:

$\Delta HA/HA = (0.67 \pm 0.22) + (1.18 \pm 0.07)\Delta LA/LA$ (p1084), i.e.

$HA2/HA1 = 0.5 + 1.2\ (LA2/LA1)$ ...4

This model does not successfully predict that the expansion of hole area ceases when leaf expansion ceases (when LA2 = LA1, HA2 = 1.7 HA1), and predicts that holes grow faster than leaves (if leaf area doubles, the final hole is 2.9 times the initial hole). In contrast, my model (equation 3) does successfully predict that HA2 = HA1 when

LA2 = LA1, and also predicts that holes grow more slowly than the leaves in which they are made (for a doubling of leaf area, the final hole will be only 1.7 times the leaf area). For many ecological studies these differences may not be critical and either model may be adequate, particularly if leaves of the same age, damaged at the same time, are being compared. Problems may arise when comparisons are attempted between fully expanded leaves which were damaged when they were young, and leaves which were damaged after they had expanded. In this case I predict that proportional damage measured on the first set of leaves would underestimate the proportional damage which actually occurred. The degree of this underestimation will be greatest for damage incurred by very young leaves, the leaf area of which will change most during expansion.

LONGTERM SAMPLING OF LEAVES

Three different measures were recorded for each leaf on each sampling occasion. These were its potential area in the absence of any damage (PA), its actual area (AA), and the area of any new damage sustained in the interval since the last recording occasion (NDA). A second measure of damage, cumulated damage area (CDA), was calculated from the difference between PA and AA for each leaf. Both measures of damage were recorded as areas, and as percentages of PA (i.e. NDP = NDA/PA x 100; CDP = CDA/PA x 100).

In the long term samples I was sometimes able to identify whole leaves which were lost when they senesced (leaves which were classified as 'old' on the last occasion when they were measured, and had not sustained recent insect damage), but I was never able to distinguish between leaves totally eaten by insects and those lost because of other factors. Many young leaves particularly, disappeared from the sample between measuring occasions. Some of the remaining young leaves had sustained severe insect damage, and some others showed signs of wind damage and desiccation, so I could only speculate about the fate of those which were missing. Thus I calculated annual measures of damage for three populations of leaves; those leaves which had been partially damaged but retained on the trees (P), partially damaged leaves plus those leaves missing for unknown reasons (P+M),

and partially damaged leaves plus all the leaves which were totally lost from the sample, including those which senesced (P+M+S).

REMOVAL OF PARTS OF LEAVES AND COMPLETE REMOVAL OF LEAVES. Cumulated damage measured on discrete samples, in contrast to measurements of longterm samples, usually only measures damage of less than 100% per leaf. Leaves which are totally removed by insects are usually not included. The estimates presented by Journet (1981), for damage to leaves of E. blakelyi, are an exception. Journet thought that most leaf abscission occurring on the trees he studied was the result of insect damage. When he included abscissed leaves in his estimates of annual foliage loss, percentage loss increased from 40% (partial leaf damage only) to 70% (including leaf scars).

Of the total percentage of leaf area lost from the trees in my sample during the year (45.3%, Table 8), approximately half was the result of natural senescence (45.3% - 21.7% = 23.6%). Three quarters of the remaining leaf area lost could not be directly attributed to insects, so that leaf area known to be damaged by insects during the year was only 6.2% of the leaf area sampled. This contrasts with the total cumulated damage per tree, which was about 61% (Table 8), a figure in closer agreement with Journet's (1981) estimate of 70%, which was also a cumulated measure. However, of this cumulated total the only damage which I was confident had actually been caused by insects was a mere 15.7%.

ACTUAL AND CUMULATED DAMAGE. The cumulated damage measured on leaves in the sample which retained on the trees for the whole year of the study was about double the actual new damage which these leaves incurred during the year of measurement (Table 8); the difference was the amount of damage the leaves must have incurred in previous growing seasons. Measures of herbivory obtained from discrete samples always relate to cumulated damage. My results indicate the potential for such measures to substantially overestimate annual herbivory losses from leaves which live for more than one year.

MEAN DAMAGE PER LEAF AND MEAN DAMAGE PER TREE. Estimates of the average values of damage sustained by whole tree canopies can be calculated from data about individual leaves in two ways; either as

the average damage per leaf for each tree (Σ percent leaf area damaged per leaf / number of leaves in the sample), or as the percentage of the foliar area of each tree which is damaged (Σ damage area for all leaves in the sample / Σ potential area of those leaves x 100). Most authors simply refer to percentage damage, without stating how the value was derived.

The two values will only closely approximate each other if leaves of all sizes, are, on average, equally damaged. This was apparently not the case for the four trees studied here, since the percentage leaf area damaged per tree was usually lower than the mean damage per leaf for the trees (Table 8). Thus smaller leaves must, on average, have sustained higher proportional damage, and the mean of the damage per leaf does not accurately represent the area lost from the trees' canopies. If the small leaves which were damaged were small because they were not fully grown at the time of damage, then the comparative growth rates of the holes and leaves become important. Leaves grow faster than their contained holes (see earlier discussion). Thus if young leaves are, on average, more damaged than fully grown leaves, then the mean damage per leaf at the time of damage (NDP/leaf; P leaves) will overestimate canopy damage, but the mean damage per leaf measured after the damaged leaves have finished growing (CDP/leaf; P leaves) will underestimate actual damage sustained to the leaf area of the canopy. Such a pattern would explain the damage values calculated in this study (Table 8). Since many insects feeding on eucalypts have definite preferences for particular ages (and therefore sizes) of leaves (Carne & Taylor 1978), there is clearly a need for authors to state how their canopy herbivory rates were calculated.

A second disadvantage of using mean area damaged per leaf is that this assumes that the frequency distribution of percentage loss per leaf approximates a normal distribution. This was not the case in this study. Instead, many leaves were only a little damaged, if at all, while the numbers of more heavily damaged leaves were more variable (e.g. Table 2 & Fig.1). Attempts to impart symmetry to these heavily skewed distributions using standard transformations (log, square root, reciprocal, arcsine) were not successful, indicating that the mean is not an appropriate measure of the their central tendency.

Thus for both these reasons it is preferable to express canopy herbivory as a mean value per tree, rather than per leaf.

DISCRETE SAMPLING OF LEAVES

The discrete and longterm samples were not directly comparable, since they were drawn from different trees (though in the same stand). In addition the longterm samples were chosen from the canopy aspect most likely to sustain damage, while the discrete samples were collected from both north and south sides of the canopies. Also, discretely sampled leaves were assessed for damage by visual estimation, rather than digitizer measurements. (This had the advantage of relative speed and allowed a greater number of trees to be sampled.) Notwithstanding these differences, at the beginning of the study the leaves in the discrete sample and those in the longterm sample had both sustained similar amounts of damage (Table 9; $t=1.112$; $df=12$; $P>0.10$).

However the estimate derived from the discrete sample of losses to herbivory in the 1982-3 growing season was significantly higher than the actual damage sustained by leaves in the longterm sample during that year (Table 9, Sep.1983; $t=3.803$; $df=12$; $P<0.01$). This was probably because the cumulated damage measured on the leaves in the discrete sample also included some damage incurred in previous growing seasons (see earlier discussion). It was usually possible to distinguish between leaves on the same shoot which had expanded during different growth flushes, because they tended to be separated by thickened growth rings on the stem. However at least five growth flushes occurred during the 1982-3 growing season (Landsberg submitted b), making it difficult to judge the timing of leaf expansion with any precision. When I excluded those leaves that I judged to have expanded in previous growing seasons from the discrete sample, the resulting estimate of annual herbivory loss was still significantly higher the actual damage sustained by leaves in the longterm sample (Table 9; $t=2.543$; $df=12$; $P<0.05$). Thus I had probably not been successful in confining the discrete sample to only those leaves damaged in the 1982-3 growing season.

CONCLUSIONS

Measurement of insect herbivory, on eucalypts or on other species, is labour intensive, and is therefore usually time-limited. Inevitably a compromise is reached between gaining detailed knowledge about a limited sample and increasing sample size at the expense of detail.

The fastest method of assessing canopy herbivory, and therefore the one with the potential to sample most trees, is visual assessment of the whole canopy. For the trees in this sample there was good correlation between canopy condition and insect damage. Thus other trees in the woodlot could be assessed for canopy condition with a reasonable expectation that it would reflect the extent of insect damage their leaves sustain. Unfortunately factors apart from insect damage can cause canopy deterioration (e.g. pathogens, drought, fire, nutritional imbalances), so that good correlation between insect damage and canopy condition cannot be assumed to be generally true.

If leaves are sampled from canopies and individually assessed for damage, the fastest method is visual estimation into damage categories. Operators tend to overestimate damage, but are very consistent in their estimates. When damage categories are calibrated against measured values of damage, visual estimations and measured values of proportional damage are in close agreement.

The derivation of proportional damage by insects sustained by whole tree canopies from assessments of damage made on individual leaves can give very different values, depending on the method used. The preferred method of expressing damage, since it makes no assumptions about the frequency distributions of damage per leaf, is to calculate the ratio of the sum of the total area of damage sustained by a sample of leaves, to the sum of the total potential area of the leaves in that sample. The least preferred method is to calculate the mean of the proportion of each leaf damaged for the canopy sample. This method makes two assumptions about the frequency distribution of damage per leaf within a sample of leaves: that the

distribution of the size of leaves damaged approximates to the distribution of the size of leaves in the sample; and that the frequency distribution of damage per leaf for leaves in the sample approximates to a normal distribution. These assumptions are seldom verified; in my study they were not valid.

This does not mean that data on proportional damage per leaf cannot be used to compare canopies. Problems of unequal representation of proportional damage in some size classes of leaves can be avoided by treating leaves of different sizes (or ages, if this is appropriate) separately in analyses. Problems of severe departure from normality in the frequency distribution of damage per leaf can be overcome by using a more appropriate measure of central tendency than the mean (e.g. the median), or by restricting statistical comparisons to the actual frequency distributions of damage per leaf for the samples of leaves from different canopies.

Discrete sampling of leaves from canopies is much faster than longterm sampling, and so allows more trees to be sampled. Also more canopy positions are accessible for sampling. Against this there is a loss of resolution of canopy dynamics when samples are collected discretely, compared with longterm studies.

In this study, annual herbivory calculated for discrete samples of leaves judged to have expanded during the current growing season was higher than annual herbivory calculated from longterm samples. Two main factors can cause annual herbivory calculated from discrete samples in this way to misrepresent actual new damage incurred during a year. If leaves which were damaged in previous growing seasons are included in the sample, then the discrete estimate will overestimate actual damage. Against this, if a significant proportion of the damage is sustained by young leaves which continue to expand after they are damaged, but which are not measured till they are fully expanded, then there will be a tendency for the calculation of annual proportional herbivory from discrete samples to underestimate actual leaf damage. This is because holes in young leaves grow more slowly than do the leaves in which they are made. Apparently the first of these factors was more important during my study.

These differences highlight the extent to which methods of measuring and calculating herbivory influence the values obtained, for trees in the same stand and even for the same stand. They illustrate both the need for authors to describe fully how the measures they quote are obtained, and also the need for caution in drawing conclusions from any comparisons between studies in which different methods were used.

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Table 1. Design of 'growing holes' experiment.

Stratum	Factor	No. of replicates in each level of the factor	Degrees of freedom
Tree	Tree Age (TA)	5 seedlings, 5 saplings, & 5 adults	TA = 2 error = 12 total = 14
Tree. leaf	Leaf Age (LA)	3 small young leaves, 3 larger young leaves, & 3 nearly mature leaves	LA = 2 TA.LA = 4 error = 114 total = 134
Tree. leaf. hole	Position of hole (HP)	1 in the tip, 1 in the middle, & 1 in the base	HP = 2 TA.HP = 4 LA.HP = 4 TA.LA.HP = 6 error = 254 total = 404

Table 2. Average values of damage measured on a digitizer of the leaves assigned to different damage categories by each operator.

Damage categories[1]	Measured damage (%)[2]: Operator SA	Operator JL
'none'	0.0 ± 0.0 (98)	0.0 ± 0.0 (87)
'a little' (5%)	1.3 ± 0.9 (129)	1.4 ± 0.4 (118)
'an eighth' (12.5%)	8.2 ± 2.5 (74)	7.9 ± 3.1 (86)
'a quarter' (25%)	20.7 ± 3.3 (69)	21.5 ± 1.8 (77)
'half' (50%)	38.8 ± 8.9 (53)	46.3 ± 5.2 (78)
'three quarters' (75%)	60.4 ± 4.9 (39)	68.1 ± 4.2 (34)
'most' (99%)	80.0 ± 4.6 (38)	84.2 ± 6.1 (20)

[1] Nominal midpoints in parenthesis

[2] Measured areas are recorded as means ± standard deviations (number of leaves assigned to that category).

Table 3. Digitizer-measured and visually estimated values of mean area of foliage damaged per tree.

Sample[1]	Visually estimated damage (%)[2]: SA1	SA2	JL	Measured damage (%)[3]
1 (last)	5.9	6.7	12.8	6.4±10
1 (curr)	3.3	4.4	7.9	3.9± 7
2	5.5	5.9	9.7	4.5± 7
3	9.8	8.9	11.8	9.0±13
101	9.8	10.7	15.2	11.1±18
102	46.5	47.6	45.0	44.5±25
103	9.4	10.2	11.1	8.6±14
104	7.7	7.6	8.4	8.2±15
302	33.1	34.5	37.3	32.3±24
303	23.9	20.3	27.3	19.3±15

1 Sample numbers <100 refer to healthy trees; 100-300 to dieback trees; >300 to artificially defoliated trees. (Last) means previous season's growth; all other samples are of current season's growth.

2 (Mean) estimated damage = $\Sigma fx / \Sigma f$, where x is the calibrated midpoint of each category for each operator (from table 2), and f is the number of leaves in each category.

3 (Mean) measured damage = $\Sigma x / n$, where x is the percentage of each leaf damaged and n is the number of leaves in a sample ($n = \Sigma f$).

Table 4. Coefficients associated with the change in leaf area from the additive models (LA2-LA1).

Hole position	Leaf age: Small young	Large young	Nearly mature
tip	.011 ± .003	.0002 ± .004	.0028 ± .002
middle	.035 ± .003	.016 ± .002	.0087 ± .002
base	.036 ± .100	.014 ± .003	.0048 ± .001

(Estimates given as $\beta \pm$ S.E.)

Table 5. Coefficients associated with the change in leaf area from the multiplicative models (lnLA2-lnLA1).

Hole position	Leaf age: Small young	Large young	Nearly mature
tip	.31 ± 10	.084 ± 17	.43 ± 31
middle	.72 ± 11	.73 ± 12	.67 ± 24
base	.68 ± 10	.71 ± 14	.58 ± 22

Table 6. Regression coefficients for the best additive model.

Term	Coefficient	S.E.
constant	0.22	0.03
LA1	-0.021	0.003
LA2	0.034	0.002
leaf age 2	0.13	0.04
leaf age 3	0.12	0.04
LA2.leaf age 2	-0.019	0.002
LA2.leaf age 3	-0.017	0.003

Percentage variance accounted for: 74.3

Plot of residual against fitted values: increasing scatter of residuals as fitted values increase.

Table 7. Regression coefficients for the best multiplicative model.

Term	Coefficient	S.E.
constant	-1.29	0.02
(lnLA2-lnLA1)	0.76	0.03

Percentage variance accounted for: 67.5

Plot of residual against fitted values: random scatter

Table 8. Different measures of insect damage sustained by leaves in the longterm sample between October 1982 and September 1983.

Leaf population[1]	Actual damage sustained: NDP /leaf[2]	NDP /tree[3]	Cumulated damage measured: CDP /leaf[4]	CDP /tree[5]
P+M+S	55.6±6.3	45.3± 5.3	63.2±5.3	61.0± 8.5
P+M	43.5±5.7	21.7±10.3	51.0±7.6	37.1±16.1
P	8.4±2.4	6.2± 1.0	13.7±6.9	15.7± 3.8

All values recorded as mean of 4 trees ± standard deviation.

1 P refers to partially damaged leaves, S to senescent leaves, and M refers to leaves missing for unknown reasons.

2 Mean percentage new damage per leaf, calculated as Σ NDP per leaf / number of leaves.

3 Mean percentage actual damage of the tree samples, calculated as Σ (NDA per leaf) / Σ (PA per leaf) x 100, summed for all leaves in the sample. (NDA = new damage area, PA = potential leaf area).

4 Mean percentage cumulated damage per leaf, calculated as ΣCDP per leaf / number of leaves in the sample.

5 Mean percentage cumulated damage of the tree samples, calculated as Σ (CDA per leaf) / Σ (PA per leaf) x 100, for all leaves in the sample (CDA = cumulated damage area).

Table 9. Different measures of insect damage sustained by leaves in the discrete sample, and comparable measures for the longterm sample*.

Date collected	Type of sample	Mean % damage per tree
Oct.1982	Discrete, all leaves	15.7±3.5
Oct.1982	Longterm, all leaves	17.1±7.6
Sep.1983	Discrete, all leaves	10.7±5.0
Sep.1983	Discrete, leaves expanded during current season	9.4±5.7
Oct.1982-83	Longterm, damage incurred during current season	6.2±1.0

* Discrete samples were collected from north and south canopy positions of 10 trees; longterm samples were in the northern side of the canopies of 4 other trees in the same stand.

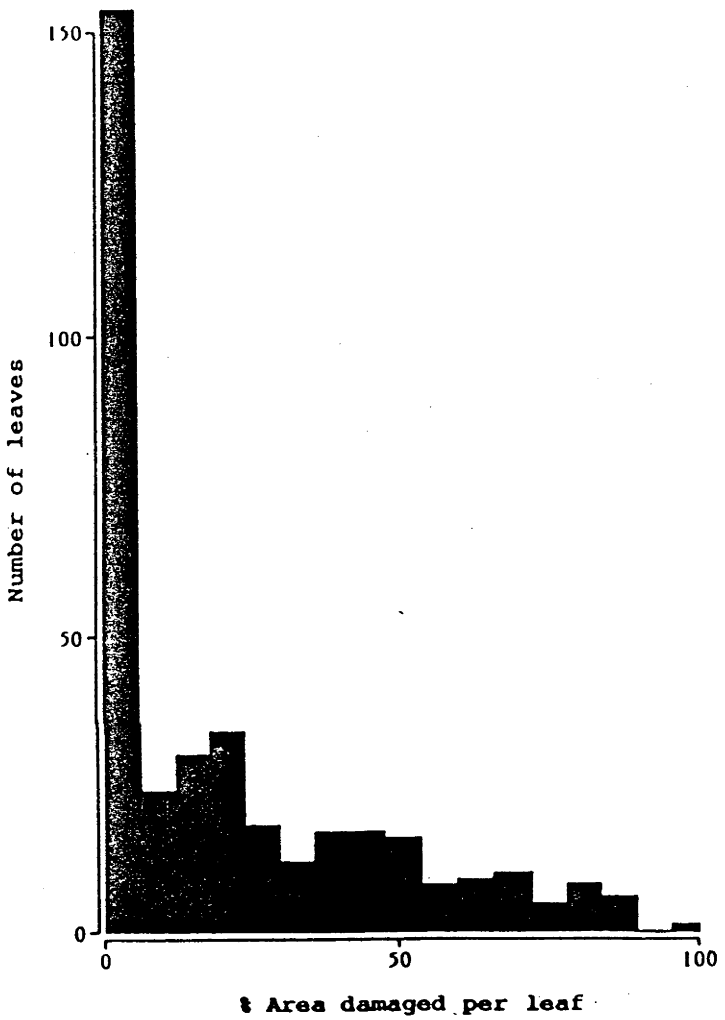

Fig. 1. Frequency distribution of damage per leaf for all leaves in the longterm sample on the first sampling occasion.

DIEBACK OF RURAL EUCALYPTS: TREE PHENOLOGY AND DAMAGE CAUSED BY LEAF FEEDING INSECTS

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ABSTRACT

Tree phenology, and the extent of insect damage to the foliage of healthy and dieback-affected eucalypts, were monitored for three growing seasons, on pastoral properties in the ACT. Leaves from the dieback trees tended to be younger than those from nearby healthy trees. Leaf longevity was similar on both dieback and healthy trees, but more leaves were initiated on the dieback trees, which were also less active reproductively. During the study most leaf damage was caused by chewing insects. Foliage from the dieback trees was usually more damaged than was that from the healthy trees. Young leaves accumulated damage at a much faster rate than older leaves, and this probably contributed to the relatively greater damage sustained by the dieback trees. However foliage from dieback trees was also more damaged than was foliage of similar age from healthy trees: when generalized linear models were used to equalize the effects of differences in tree phenology, the resulting adjusted estimates of foliar damage were still higher for the dieback trees.

INTRODUCTION

Although damage by insects is frequently cited as an important factor in the widespread dieback of native trees in pastoral areas of Australia (Kile 1981), this belief is based on surprisingly few studies of the ecology of dieback of rural trees. In contrast, the autecology of many of the species of insects that periodically cause severe defoliation of woodland eucalypts has been well researched (e.g. Campbell 1962; Carne 1962, 1965 & 1966; Carne et al. 1974; Clark & Dallwitz 1974; Harris 1974; Mazanec 1974; Wallace 1970; White 1971). It is often concluded, by extrapolating from such studies, that damage caused by leaf feeding insects is a critical factor in the gradual decline in vigour which characterizes rural tree dieback (e.g. Breckwoldt 1986; Anon. 1985).

Detailed studies have not always supported this view. For example, the foliage of native trees growing on grazing properties in the Mt Lofty ranges of South Australia was less damaged by insects than was the foliage of trees growing in adjacent forests (D. Peake-Jones, University of Adelaide, pers.comm.). Insect damage was not implicated in the dieback of pine and cypress trees in exotic windbreaks in southern Victoria (J.D. Morris, Vic. Dept. Conservation Forests & Lands, pers.comm.), and did not appear to be an important factor in the dieback of river red gums on farms in western Victoria (C. Clifton, University of Melbourne, pers.comm.).

However, insect grazing has been implicated in rural tree dieback in the New England Tablelands of NSW (Mackay et al. 1984), and in south eastern Queensland (Landsberg & Wylie 1983). In the early stages of the development of dieback in these regions, tree decline is patchy rather than extensive. Trees with severe dieback are commonly found growing adjacent to healthy trees which appear, in other respects, very similar to the trees with dieback.

For a number of eucalypt-insect systems, it has long been known that trees of the same species are not equally favourable for the particular insect species for which they are host, and that this variation in susceptibility is remarkably consistent through time (e.g. Carne 1965 & 1966; Carne et al. 1974; Clark 1962; Journet 1980;

Mazanec 1974). The reasons for this are not always well understood. Carne (1965) found that a major factor determining the susceptibility of individual trees to defoliation by sawfly larvae was the history of previous defoliation of the trees. Trees which were severely defoliated in one season frequently shed their remaining foliage and replaced their entire canopies with a synchronous flush of new growth that was highly susceptible to subsequent reinfestation. In this way a positive feedback loop was initiated, and previously unfavourable or unattractive trees became chronically infested with sawfly larvae as a result of the phenological changes induced by a single severe defoliation. Landsberg and Wylie (1983) proposed that a similar mechanism may be involved when dieback of rural trees is associated with increased grazing by insects.

Dieback is widespread among native trees in the pastoral zones of the Southern Tablelands of New South Wales and the Australian Capital Territory (Hogg & Wittmark 1983). In this paper I demonstrate that dieback of Eucalyptus blakelyi Maiden, one of the common species of eucalypt on pastoral lands in this region, is increasing in severity, and is associated with increased grazing by a number of different insect species. I also illustrate that variation in the susceptibility of individual trees to insect damage reflects both differing tree phenologies, and intrinsic differences between trees in the susceptibility of foliage of similar age.

METHODS

STUDY SITES AND TREES

Data were collected from E. blakelyi trees growing on two pastoral properties at Hall in the Australian Capital Territory, from September 1982 to January 1985. Both sites are managed for grazing of sheep and cattle. Site 1 is a semi-cleared remnant of native woodland on a gentle hillslope with some rock outcrop; the pasture is dominated by Phalaris sp. Site 2 consists of scattered shade trees amongst mixed, unimproved pasture in a valley bottom. E. blakelyi is the dominant tree species at both sites but E. melliodora A.Cunn. ex Schau. is also

common. This association occurs extensively on the grazing lands of the slopes and tablelands of New South Wales (Milton Moore 1975), and is very susceptible to rural tree dieback (Duggin 1981).

The vitality of the canopies of trees at the sites varied markedly. At the beginning of the study I classified trees as 'healthy' or 'dieback' from an assessment of crown size, density, epicormic growth and dead branches (Landsberg & Wylie 1983; modified from Grimes 1978). The condition of the canopies of many of the trees growing in the paddocks at site 1 had also been assessed in 1973 and in 1982, by a firm of Environmental Consultants (David Hogg Pty. Ltd., Canberra), to provide data for landscape planning. I used their data to determine if the condition of tree canopies had deteriorated in the intervening years.

SAMPLING

Leaves were sampled for assessment of extent of insect damage in two ways, by 'longterm' sampling and by 'discrete' sampling (Lowman 1984 & 1985; Landsberg submitted a). Longterm sampling involved tagging 20 terminal branchlets on three dieback and three healthy mature trees at site 1 only, and tracing the outlines of all leaves (initially about five) distal to the tag. Changes to the leaves, and to any new leaves which emerged distal to the tags, were recorded on the tracings on subsequent sampling occasions. Measurements were made at about fortnightly intervals during the growing season (September 1982 to March 1983) and monthly thereafter until the beginning of the next growing season in September 1983.

Discrete samples were collected from both sites (from five healthy and five dieback trees at each) at about monthly intervals during the same period, to coincide with measurements of longterm samples. A branch was cut with pole pruners from the upper and lower north and south canopy positions of each tree, and five terminal branchlets carrying about five leaves each were cut from each branch, so that about 100 leaves were sampled from each tree. After the cessation of longterm sampling, discrete sampling was continued at site 1 only, at two to three month intervals until January 1985. These samples were

collected from the 10 trees monitored in the first year plus the six trees which had been earlier monitored by longterm sampling.

PHENOLOGY

Sampled leaves were classified according to apparent age, (young, nearly mature, mature 1, mature 2, old 1, old 2) based on their appearance and their pattern of emergence along a shoot. The shoots were further classified according to their form, as either 'epicormic' or 'adult', and shoots which were epicormic in origin as having arisen in the most recent growing season (E1) or up to four growing seasons previously (E4). This was possible because thickened growth rings on the stems separated each growth flush. Thus a total of 30 combinations of age and form categories was theoretically possible, although in practice there were usually only from one to four age categories and one or two form categories represented on any particular tree at any time.

The numbers of leaves from each tree in each category were recorded, as was the presence of any reproductive organs (flower buds, flowers or fruits) on sampled branches. In addition the average leaf area of the leaves in the longterm sample was measured on a digitizing board, by tracing the leaves' estimated original outlines on each occasion until each leaf had fully expanded. The areas of a subsample of the leaves collected discretely were also measured. A maximum of 20 leaves was measured in each age/form category from each tree, every second month for the first year of sampling.

EXTENT OF DAMAGE OF LEAVES BY INSECTS

Damage to leaves in the discrete samples was visually estimated, by scoring the number of leaves which were assigned to each of six damage ranks ranging from 'no damage' to 'most of leaf damaged'. These ranks were calibrated against measured values of damage, and damage was calculated for each age/form category represented on each tree, as the proportion of that sample damaged (Landsberg submitted a).

Six different types of damage were recorded: removal of leaf material, damage caused by sapsucking insects, damage caused by skeletonizing or mining insects, damage caused by gall forming insects, necrotic damage, and any other types of damage. 'Removal' referred only to removal of parts of leaves. Leaves which had been completely removed, i.e. leaf scars, were not assessed for the discrete samples. 'Damage' by sapsucking and gallforming insects was recorded as the proportion of leaf or stem occupied by the insects concerned or the resulting galls, and is therefore an underestimate of their likely impact on tree growth. Since the extent of this impact is largely unknown this measure was used as an index of damage to allow relative comparisons to be made.

For the longterm samples, only the damage caused by removal of leaf material (including leaves which were completely removed) was measured. This was done by tracing leaf outlines on a digitizing board connected to a desk-top microcomputer (Ohmart & Stewart 1985). Actual leaf outlines, estimated leaf outlines in the absence of any damage, and outlines of holes were traced. This allowed computation of the potential area in the absence of damage and the actual, undamaged area of each leaf. The cumulated area damaged was calculated as the difference between potential and actual areas. The area of new damage incurred in the interval between sampling occasions was measured separately, and recorded as a newly damaged area on the date it was first noted. Proportional damage was calculated from each of these measures for foliage in each age/form category on each sample date, as the ratio of the total area of damage for each category to the total potential area of leaves in that category (Landsberg submitted a).

INSECT POPULATIONS

Estimates of the relative abundance of the main groups of leaf feeding insects were made on E. blakelyi saplings (10 at each site for the first year, then 10 at site 1 only), after scanning the foliage in each quadrat of each tree for several minutes. The insects observed were identified and their abundance was rated on an ordinal scale, as

'rare', 'apparent', 'common' or 'abundant'. Estimates were made between 10am and 1pm on days on which discrete samples were collected.

TREATMENT OF DATA

TREE HEALTH. The assessment ratings used in 1973 and 1982 differed slightly, so I assigned numbers to equivalent ranks for analysis. Trees rated as 'outstanding', 'excellent' or 'good' in 1973 were treated as equivalent to a rating of 'good' in 1982 (rank=10); trees rated as 'fair' in either year were assigned a rank of 9; trees rated 'to be removed' in 1973 were treated as equivalent to a rating of 'poor' in 1982 (rank=8); and trees rated as 'dead' in 1982 were assigned a rank of 7. The sample comprised 130 E. blakelyi trees. I tested the hypothesis that the condition of the trees' canopies had declined between 1973 and 1982 with a Wilcoxon matched-pairs signed-ranks test of these ranks (Siegel 1956).

PHENOLOGY. Leaf longevity, and the average time interval represented by each age category, were calculated from the data on leaves in the longterm sample. The significance of differences between the groups of dieback and healthy trees was determined by t test. Data were first log transformed to stabilize variances (Snedecor & Cochrane 1980).

Leaves on dieback trees appeared younger than leaves on healthy trees. I tested this hypothesis by applying the Kolmogorov-Smirnov two-sample test (one-tailed) to the data collected by discrete sampling (Siegel 1956). The K-S D statistic was calculated from cumulative frequency distributions of all the leaves collected from each group of trees, and scored in ranked categories of young, nearly mature, mature and old. (The last two categories were formed by combining the data from the mature 1 & 2 and old 1 & 2 categories.)

'Age cohorts' of leaves which emerged during the same sampling interval were identified from the longterm data, and the number and total leaf area of leaves in each cohort were calculated for both dieback and healthy trees. The numbers of leaves which disappeared between sampling occasions were also recorded. The fate of these

leaves was unknown, despite detailed observations. They may have been totally eaten, or they may have abscissed because they were heavily damaged by herbivores, wind or desiccation, or pathogens. Flushes of leaf growth were patchy within each canopy and were not well synchronized between trees. Since no cohort of leaves related to more than three of the six trees being monitored, statistical comparisons between the groups of trees were not justified for these data.

DAMAGE OF LEAVES BY INSECTS: Statistical comparisons were only attempted between the dieback and healthy trees in the discrete sample. This sample included a larger number of trees than did the longterm sample (20 compared with six), and leaves were sampled from more canopy positions on each tree. There were, however, a variable number of estimates of damage relating to each tree, depending on the number of age/form categories represented, and in each category the number of leaves also varied (from 0 to 50). Because numbers were unequal in the age and form categories, and these factors were not orthogonal, the data were analyzed by fitting a series of regression models using generalized linear modelling subroutines from Genstat (Alvey et al. 1982).

The procedure used was analogous to analyzing a split plot design of experiment, in which the factors contributing to within tree variance (tree, leaf age, leaf form, and interactions between leaf age, form and tree health) were analogous to subplots and the factors contributing to variation between trees (tree health and site) were analogous to main plots. Analyses were repeated for each type of damage and for each sampling date.

'Unadjusted means' (Tables 5-7) were estimated by fitting constants for each level of a factor for tree, weighted for the number of leaves actually measured, so that the estimated constants for each level of the tree factor represented mean values for each tree. Since the number of trees was balanced for site and tree health, the significance of the effect of these factors was tested by a standard analysis of variance of the tree constants. No adjustment was made for any differences in phenology in this first set of analyses.

A second series of models were fitted to test the significance of factors related to tree phenology (leaf age, form, and interactions) in contributing to the variance in leaf damage ('significant model terms' in Tables 5-7), and to determine how the incorporation of any significant phenological factors affected the comparison of leaf damage between dieback and healthy trees. Because of the number of terms and interactions involved it was impractical to fit all possible factor combinations. Preliminary analyses had shown that leaf age was more often significant in explaining levels of leaf damage than leaf form, so the significance of the terms involving interactions was only tested in models which already incorporated the leaf age factor. The most complex model fitted was:

$$\begin{aligned} \text{damage}_{ijk} &= (\mu + \text{health}_i + \delta_{ij}) + \text{age}_k + \text{form}_l + (\text{health x age})_{ik} + \\ &\quad (\text{health x form})_{il} + (\text{age x form})_{kl} + \varepsilon_{ijkl} \\ &= \text{tree}_{ij} + \text{age}_k + \text{form}_l + (\text{health x age})_{ik} + (\text{health x} \\ &\quad \text{form})_{il} + (\text{age x form})_{kl} + \varepsilon_{ijkl} \end{aligned} \qquad \ldots 1$$

where ε_{ijkl} is a random effect contributing to within-tree variation; δ_{ij} is a random effect contributing to between-tree variation; and i (= 1,2), k (= 1...6) & l (= 1...5) are the levels of the factors tree health, leaf age and leaf form, respectively.

The terms were fitted stepwise starting with tree, and the significance of each new term, adjusted for the terms preceding it, was determined from an F test, by calculating F as the change in mean square divided by the residual square of the fuller model (Alvey et al. 1982). 'Adjusted means' (Tables 5-7) were calculated by fitting constants for the tree factor, as before, and then incorporating into the regression any other significant terms from equation 1. These adjusted means differed from the unadjusted ones because the effects of any of the factors which contributed significantly to within-tree variation in leaf damage were equalized in the final estimate. The significance of tree health and site in contributing to the variance in the adjusted means was tested using ANOVA, as before.

The nature of the variation in damage to foliage within trees was investigated in two ways. Rates of development of damage were calculated for the discrete sample from damage estimates for each age category, averaged over all sampling occasions. These means represented cumulated proportional damage for each age category; they were converted to rates by dividing the difference in damage estimates between each age category and the one younger by the time span represented by each category. This was repeated for both groups of trees, for each of the damage types which accounted for most of the damage. Damage development had been measured directly for the age cohorts of leaves in the longterm sample. These data are presented graphically, for those leaves which survived until they were fully mature. Actual numbers of leaves were low and unbalanced, so no statistical comparisons were attempted.

RESULTS AND DISCUSSION

TREE HEALTH

Site 1 was not judged to be badly affected by dieback in either 1973 or 1982 (median scores were 'good' in both years), but the condition of many of the trees had deteriorated between the two surveys. The rankings for 68 trees changed; 15 of these had improved and 53 had deteriorated. The overall decline in the condition of the trees was significant ($T=21$; $n=68$; $P<0.01$), indicating that dieback at the site is increasing.

PHENOLOGY

Leaves from dieback trees attained a mature appearance more quickly than leaves from healthy trees; they were classed as 'young' for about 33 days, compared with about 39 days for leaves from healthy trees (Table 1). Since insect feeding can speed senescence (e.g. Woodburn & Lewis 1973) this difference may have been related to herbivory. However there was no significant difference in the extent to which young leaves from either dieback or healthy trees were

damaged; differences were only significant when leaves were mature and old (Table 10). Leaves from dieback trees also retained a mature appearance for longer than leaves from healthy trees (about 242 days for the dieback tree leaves, compared with about 204 days for leaves from healthy trees). There was considerable variation in the time individual leaves remained 'old', and differences between dieback and healthy trees were not significant. Although leaves from both dieback and healthy trees were assessed as remaining 'nearly mature' for about 14 days this may be an overestimation, since it is also equal to the time interval between sampling occasions.

The sum of the amount of time leaves were classed in each age group is an indication of the longevity of those leaves which were retained until they naturally abscissed, but gives no indication of the likelihood of leaves being shed or removed prematurely. Leaves in the longterm sample which were retained until they appeared very old ('old 2') were shed after about 500 days, with little difference between leaves from dieback and healthy trees (Table 1). Many leaves were lost prematurely from the sample (from 40 to 100% of any age cohort), usually while they were still young, but again there was little difference between dieback and healthy trees in the proportion of the total number of initiated leaves that this represented (Table 2).

However many more leaves were initiated on the dieback trees in the longterm sample than on the healthy trees (Table 2). This may well explain the difference in age structure of leaves collected from dieback and healthy trees by discrete sampling: leaves from the dieback trees were nearly always younger (Table 3), and young leaves usually constituted a greater proportion of the total number of leaves sampled from the dieback trees (Fig.1).

Although the average area of leaves on dieback trees in the longterm sample was smaller than those on the healthy trees, the dieback trees initiated so many more leaves that this amounted to a greater potential area of foliage (Table 4; Fig.2). However, the dieback trees lost a greater proportion of this potential foliar area than did the healthy trees; thus the area which survived until after leaves had fully expanded was little different for both groups of

trees (Table 4). Therefore although both groups of trees derived a similar benefit in terms of foliar area available for photosynthesis, the metabolic costs of achieving this were greater for the dieback trees.

E. blakelyi trees tend to have a two year cycle of reproduction and replacement of foliage, alternating between seasons beginning with seeding, replacement of most leaves and flower bud production (major leaf flush season); and seasons beginning with flowering, setting of fruit and production of relatively few leaves and flower buds (minor leaf flush season) (Clark & Dallwitz 1974). Data from the discretely sampled trees shows that their major leaf growth flush occurred in the 1983-4 growing season, and that only minor flushes of leaf growth occurred during the 1982-3 and 1984-5 seasons. Flowering and setting of fruit occurred during the 1984-5 season, but was not apparent during the 1982-3 season (Fig. 1). Most of that season was under the influence of a severe drought (Landsberg 1985), and this is likely to have caused some suppression of reproductive activity. There may also have been an effect on leaf growth. The proportion of young leaves which were present on trees in January was much lower in 1983 than in 1985, suggesting that fewer leaves than normal may have been initiated during the first season of the study, and/or that a higher proportion may have been lost prematurely. (The high proportion of leaves which was lost during the 1982-3 growing season while they were still young has already been noted (Table 2).)

Notwithstanding these differences dieback trees had a higher proportion of young foliage in their canopies than did healthy trees in all three growing seasons monitored, and less evidence of reproductive activity. Fewer dieback trees produced flower buds in the first two growing seasons, none flowered in the 1983-4 season, and fewer flowered and set fruit in the 1984-5 season (Fig.1). This reduction in reproductive activity might have partially offset the relatively higher metabolic costs the dieback trees were likely to have incurred in producing foliar area available for photosynthesis.

DAMAGE OF LEAVES BY INSECTS

VARIATION BETWEEN TREES: The percentage of leaf area covered by sapsucking insects or galls, or damaged by mining and skeletonizing insects, was low throughout the study, and seldom differed significantly between dieback and healthy trees (Table 5). The only consistent trends for these types of damage occurred for galls, and leaf age was usually a significant factor in explaining variation in the proportion of leaf area they covered. They also tended to cover a higher percentage of the leaf area of healthy foliage samples (though differences were never significant). Differences between the two sites were seldom significant, but when they were trees at site 1 were usually more heavily damaged (coverage by sapsuckers and damage by skeletonizers were significantly higher at site 1 on three different occasions. Coverage by galls was higher at site 1 once, and higher at site 2 twice).

The indices used to assess damage by sapsucking and gallforming insects were underestimates of the probable true extent of the damage these insects cause, but even allowing for this, only a small proportion of the foliar area is likely to have been damaged in this study, since the indices were so very low (usually less than 1% of foliar area covered by insects or their traces). Psyllids can cause serious tissue damage and defoliation when present in high numbers (e.g. White 1970, Woodburn & Lewis 1973), but numbers fluctuate markedly (e.g. Clark & Dallwitz 1974) and were low throughout this study.

The types of damage affecting the largest proportion of foliar area were necrosis, and removal of parts of leaves by insects (Tables 6 & 7). Leaf age often contributed significantly to variation in the extent of leaf necrosis. For foliage samples collected in October and November 1982, and in February and July 1983, this appeared to be the main cause of significant differences between dieback and healthy trees in the proportion of their foliar area which was necrotic. When tree means were adjusted to equalize the variation due to leaf age, differences between the groups of trees were no longer significant (Table 6). Adjusted means differed significantly between the dieback and healthy trees on five occasions, but the direction of the

differences was not consistent. When the proportion of necrotic leaf area exceeded 10% (adjusted means), it was the dieback trees which were most affected. The estimates for the two sites differed significantly on two occasions; site 1 was the more damaged both times.

Removal of parts of leaves was the type of damage that affected the greatest proportion of leaf area (Table 7). Site differences for this category of damage were not consistent, but on the two occasions when they were significant, foliage of trees at site 1 was more damaged. However tree health did affect damage levels; foliage from dieback trees consistently had a higher percentage of leaf area removed than did foliage from healthy trees, and these differences were often significant. Leaf age was again the within-tree factor which most often significantly contributed to the variance in removal of foliar area. However, in contrast to leaf necrosis, tree means adjusted to equalize the effects of these within-tree factors remained significantly different with respect to tree health. Indeed on five occasions the significance of differences between dieback and healthy trees was actually increased after account had been taken of factors contributing to variance within trees. This suggests that there is some intrinsic difference in the susceptibility of foliage from dieback and healthy trees, and that this is in addition to the way in which differences in their phenologies affect relative susceptibilities.

VARIATION WITHIN TREES. As noted above, leaf age was the factor that most often contributed significantly to variation in extent of damage within trees. Leaf form was seldom significant in contributing to within tree variance, but this was largely due to the distribution of leaves of different forms; few trees had foliage of more than two forms present at any time. Thus there was usually insufficient variation in the form of foliage within trees to investigate its effect. This, too, was often the case with an interaction between form and tree health; dieback trees seldom had adult-form foliage and healthy trees seldom had epicormic- form foliage, so variation within trees due to this interaction could not be investigated.

The total damage which leaves accumulate during their life spans depends on both the rate of accumulation of damage and the time span which each age category represents. Leaves in this study were young for about 7% of their life spans, nearly mature for another 3%, mature for a further 46%, and old for the remaining 44% of their life spans (calculated from Table 1). The rate of accumulation of galls, necroses, and removal of leaf area was greatest when leaves were nearly mature or young (Tables 8, 9 & 10), but leaves were only in these states for about the first 10% of their life spans. Even though rates of accumulation of damage were much lower for mature and old leaves, damage continued to accumulate over the much longer time spans involved. Thus differences between the foliage of dieback and healthy trees in total damage accumulated only became significant in these longer lived age categories (Tables 8 & 10).

The rate at which leaves accumulated galls was greatest when they were nearly mature (Table 8). At all other ages the rate was low, although the rate of accumulation on dieback foliage was consistently lower for most age classes. By the time leaves were mature the foliage on healthy trees had accumulated significantly greater coverage by galls, and this difference was maintained as the leaves became old. However, both the rates of accumulation and the proportions of foliage affected were very low (Table 8), and the average proportion of foliage covered per tree never differed statistically between dieback and healthy trees (Table 5). As foliage on dieback trees aged, a greater proportion of its area was lost to herbivores (Table 10). Since some of this lost leaf area was likely to have included accumulated galls, this may partly account for the relatively lower proportional area of older foliage from dieback trees which was covered by galls.

The rate of accumulation of necrotic area was greatest when leaves were nearly mature and least when they were mature, but there was little difference between foliage from dieback and healthy trees in either the rate of development of necrosis or the proportion of foliar area which was necrotic (Table 9).

Leaf age had most impact on the development of damage caused by removal of leaf area; about 75% of this damage was incurred in the

first 10% of the leaves' life spans (Table 10). This trend was also evident in the data for age cohorts from the longterm sample. Most removal of foliar area occurred when leaves were still growing and very little removal damage was recorded once leaves had matured (Fig. 3). Although differences between foliage on dieback and healthy trees were not consistent for these longterm data, the extent to which individual leaves are damaged is highly variable (Landsberg submitted a) and the number of leaves which survived to maturity in each cohort was very small (Table 2).

Very few instances of damage were recorded on any of the leaves in the longterm sample after they had reached maturity (Fig. 3), but significant damage was incurred on the mature and old foliage in the discrete samples (Table 10), which included many more leaves. For leaves in the discrete samples the rate of accumulation of damage was consistently higher on foliage from dieback trees, and by the time the leaves had matured foliage from dieback trees had sustained significantly more damage than foliage from healthy trees. This is consistent with the results of the model fitting analysis (Table 7), which showed that estimates of proportional area removed from dieback tree foliage remained higher than those for healthy trees, even after the effect of differences in the ages of the foliage samples was taken into account.

INSECT POPULATIONS

Although many different species of insect herbivores were observed during the study (Table 11), their relative abundance varied seasonally and between years. At no time was any species present in very high numbers: the median scores of the abundance of populations were never higher than 'common', and were more usually only 'apparent' or 'rare'. Several species of leaf fungi were apparent on some saplings at various times and may have contributed to leaf necrosis. Seimatosporium cylindrosporum Swart was apparent in winter in 1984, and an undescribed species was apparent in autumn in 1983 and in winter in 1984. (This species closely resembled Phoma australis Cooke which is currently undergoing reclassification, H.J.Swart, University of Melbourne, pers.comm.).

CONCLUSIONS

Although many trees at my study sites remain healthy, the condition of many others has deteriorated over the last decade. During most of my study the foliage of trees with dieback was more damaged by insects than was the foliage of neighbouring healthy trees. A number of different insect species contributed to this damage and no insect species were present in pest proportions. Thus it appears that the dieback was associated with chronic defoliation by those species which happened to be locally common, rather than with severe defoliation by any particular species of insect.

Since young and nearly mature foliage was most susceptible to damage by insects, and since dieback trees produced proportionally more of this foliage than did healthy trees, these phenological differences must have contributed to the increased defoliation sustained by the dieback trees. They may also have constituted a positive feedback loop, sensu Carne (1965) and Landsberg and Wylie (1983), with dieback trees repeatedly replacing young foliage in response to chronic herbivory on it.

However this was not the only reason for the greater susceptibility of dieback trees to damage by insects. Foliage from dieback trees was damaged more than was foliage of similar age from healthy trees, and statistical adjustments for differing phenologies did not reduce the significance of the difference in defoliation between dieback and healthy trees. Investigations of the causes of this intrinsic difference are reported elsewhere (Landsberg 1985, and submitted c, d & f): it could be inherited, it could arise from differences in the trees' local environments, or it could be induced by previous defoliations. This intrinsic difference means that dieback trees are not maintained in a state of enhanced susceptibility to defoliation solely because of changes in their phenology. Trees with dieback could escape from a phenological feedback loop if a greater proportion of their young foliage were allowed to grow old.

This could occur, for example, after several years of very low insect numbers, or following insecticide treatment. However, recovery of this nature is unlikely to persist in the long term unless the causes of the intrinsic susceptibility of dieback trees to defoliation are also removed.

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Table 1. Time intervals represented by age categories, calculated from leaves in the longterm sample.

Age category	Time interval in days[1]: All foliage	H foliage[3]	DB foliage[4]	t value[2]
young	35±11(181)	39±13 (85)	33± 8 (96)	2.66 ***
nearly mature	14± 4 (35)	14± 4 (14)	14± 5 (21)	0.38 ns
mature 1	161±32(196)	138±42 (57)	172±17(139)	6.99 ***
mature 2	69± 7(137)	66±10 (45)	70± 5 (92)	3.28 ***
(all mature)	230	204	242	
old 1	181±64(178)	195±64(124)	147±54 (54)	1.58 ns
old 2	38±48 (35)	29±20 (24)	63±86 (11)	1.41 ns
(all old)	219	224	210	
Time interval from initiation to senescence:	498 (762)	481 (349)	499 (413)	

[1] Expressed as mean ± std.dev. (number of leaves)

[2] Calculated from log transformed data for healthy and dieback foliage; *** P<0.01, ** P<0.05, ns P>0.05

[3] Healthy trees' foliage

[4] Dieback trees' foliage

Table 2. Survival of leaves initiated in the longterm sample during the 1982-3 growing season.

Sampling date	Number of leaves surviving in each age cohort:									
	Cohort 1		Cohort 2		Cohort 3		Cohort 4		Cohort 5	
	H	DB	H	DB	H	DB	H	DB	H	DB
13 Sep.82										
3 Oct.82	8	0								
19 Oct.82	8	0								
2 Nov.82	3	0	18	141						
17 Nov.82	3	0	18	140	32	31				
2 Dec.82	1	0	15	108	32	30	20	18		
14 Dec.82	1	0	8	92	26	22	19	17	0	17
27 Dec.82	1	0	8	89	25	22	19	16	0	17
12 Jan.83	0	0	8	88	24	20	10	7	0	13
25 Jan.83	0	0	8	82	24	17	8	5	0	3
8 Feb.83	0	0	8	80	22	15	8	4	0	3
24 Feb.83	0	0	8	77	21	15	8	3	0	2
9 Mar.83	0	0	8	77	20	15	7	3	0	2
7 Apr.83	0	0	8	75	20	15	7	3	0	2
4 May 83	0	0	8	74	19	15	7	3	0	2
14 Jun.83	0	0	8	74	19	15	7	3	0	2
25 Jul.83	0	0	8	70	18	14	6	3	0	2
7 Sep.83	0	0	8	69	18	14	6	3	0	2
Percentage of leaves lost prematurely:										
	100	-	55.6	51.1	43.8	54.8	70.0	83.3	-	88.2

H refers to leaves on healthy trees, DB refers to leaves on dieback trees. 78 leaves were initiated on healthy trees; 32 survived to the end of the growing season and 58.9% were lost prematurely. 207 leaves were initiated on the dieback trees; 88 of these survived and 57.5% were lost prematurely.

Table 3. Kolmogorov-Smirnov test of whether leaves collected from dieback trees are younger than leaves collected from healthy trees.

Sampling date	Test statistic	Sampling date	Test statistic
13 Sep.1982	19.01 ***	14 Jun.1983	24.36 ***
3 Oct.1982	38.55 ***	25 Jul.1983	41.71 ***
2 Nov.1982	35.04 ***	7 Sep.1983	5.11 *
2 Dec.1982	15.38 ***	12 Nov.1983	6.76 **
27 Dec.1982	34.82 ***	5 Jan.1984	22.02 ***
25 Jan.1983	32.53 ***	1 Mar.1984	5.24 *
24 Feb.1983	47.17 ***	11 May 1984	0.46 ns
9 Mar.1983	13.60 ***	3 Aug.1984	0.00 ns
7 Apr 1983	38.22 ***	24 Sep.1984	0.00 ns
4 May 1983	11.70 ***	8 Jan.1985	27.33 ***

Test statistic = $4D^2n_-n_+/(n_-+n_+)$, where D is the maximum difference between dieback and healthy trees in the observed cumulative step function for the number of leaves in each age class. The test statistic has a chi-square distribution with df=2.
*** P<0.01, ** P<0.05, * P<0.10, ns P>.10

Table 4. Areas of leaves initiated in the longterm sample during the 1982-3 growing season.

Leaf areas (mm^2):	Tree health:	Age cohort: 1	2	3	4	5	Total for all cohorts
Mean mature leaf area[1]	H	364	1219	1576	922	-	-
	DB	-	642	653	486	350	-
Potential area initiated[2]	H	2912	21942	50432	18440	0	93726
	DB	0	90522	20243	8748	5950	125463
Actual area surviving	H	0	8801	24526	4611	0	37938
	DB	0	38074	6101	966	177	45318
Leaf area lost (%)[3]	H	100	60	51	75	-	59
	DB	-	58	70	89	97	64

[1] Calculated as the sum of the areas of fully expanded leaves divided by the number of those leaves.

[2] Calculated from the product of the number of leaves initiated in each cohort and the mean area of mature leaves in that cohort.

[3] Includes leaves lost prematurely and leaf area removed from remaining leaves.

Table 5. Mean values, for the groups of discretely sampled dieback and healthy trees, of the percentage of foliar area with minor forms of damage. Sampling dates for which neither mean exceeded 1% are not tabulated.

Sampling date	Unadjusted means[1] H	DB	sig.[4]	Significant model terms[2]	Adjusted means[3] H	DB	sig.[4]
A. Foliage covered by sapsucking insects.							
13 Sep.82	3.1	3.3	ns	-	-		
3 Oct.82	1.3	1.0	ns	A	1.0	0.7	ns
2 Nov.82	0.7	1.1	ns	A,F,AxF,AxH	0.5	1.3	ns
B. Damage by mining and skeletonizing insects.							
13 Sep.82	1.4	1.0	ns	A	2.3	2.4	ns
3 Oct.82	1.9	0.6	**	-	-		
C. Foliage covered by galls.							
13 Sep.82	2.4	1.6	ns	A	3.1	2.7	ns
2 Nov.82	0.5	0.3	ns	A	1.3	1.1	ns
9 Mar.83	1.5	0.6	ns	A	2.2	1.8	ns
14 Jun.83	1.5	1.0	ns	A	0.9	0.7	ns
25 Jul.83	1.2	0.8	ns	-	-		
5 Jan.84	2.6	1.1	ns	A	2.2	2.1	ns

[1] Calculated from mean values for each tree, not adjusted for any differences in leaf age or form.

[2] Factors whose variation within each tree's sample significantly contributed ($P<0.10$) to variation among the trees. The factors tested were: leaf age (A), leaf form (F), their interaction with each other (AxF), and their interaction with tree health (AxH & FxH). A dash indicates that none of the factors was significant.

[3] Calculated by fitting a regression for each tree incorporating the model terms shown, so that means are adjusted to equalize the effects of these terms for between-tree comparisons. Dashes indicate that adjusted means were equivalent to unadjusted means.

[4] Significance of differences between means, from F tests; *** $P<0.01$, ** $P<0.05$, * $P<0.10$, ns $P>0.10$.

Table 6. Mean values, for the groups of discretely sampled dieback and healthy trees, of the percentage of foliar area which was necrotic.

Sampling date	Unadjusted means H	DB	sig.	Significant model terms	Adjusted means H	DB	sig.
13 Sep.82	11.2	14.5	**	A,F,AxF	10.9	22.6	***
3 Oct.82	8.8	8.1	*	A,F,AxF	9.0	8.8	ns
2 Nov.82	5.1	3.4	**	A	8.1	7.3	ns
2 Dec.82	1.9	1.3	ns	A	4.8	5.0	ns
27 Dec.82	2.8	1.1	ns	A	6.4	6.2	ns
25 Jan.83	2.9	1.4	**	A	4.5	3.5	**
24 Feb.83	4.3	2.2	*	A	7.2	6.9	ns
9 Mar.83	4.0	3.2	ns	A	7.7	6.6	ns
7 Apr.83	8.6	8.9	ns	A	12.1	15.5	ns
4 May 83	4.3	4.1	ns	A	6.0	6.6	ns
14 Jun.83	4.4	3.4	ns	A	5.5	5.6	ns
25 Jul.83	7.1	4.0	**	A	11.9	12.3	ns
7 Sep.83	6.1	3.3	*	A	6.1	3.2	*
12 Nov.83	2.8	3.3	ns	A	22.6	24.2	**
5 Jan.84	2.5	1.9	ns	A	5.9	5.9	ns
1 Mar.84	1.2	1.6	ns	-	-		
11 May 84	4.5	6.3	ns	-	-		
3 Aug.84	7.2	10.0	*	-	-		
24 Sep.84	6.1	6.5	ns	-	-		
8 Jan.85	4.0	3.7	ns	A	4.7	4.9	ns

(See Table 5 for explanation of column headings.)

Table 7. Mean values for the groups of discretely sampled dieback and healthy trees, of the percentage of foliar area removed.

Sampling date	Unadjusted means H	DB	sig.	Significant model terms	Adjusted means H	DB	sig.
13 Sep.82	18.1	21.3	ns	A	23.7	28.8	**
3 Oct.82	13.5	19.4	**	A	18.3	26.1	**
2 Nov.82	10.2	11.3	ns	A,F,AxF	18.7	21.6	ns
2 Dec.82	8.4	9.1	ns	A	14.8	17.0	ns
27 Dec.82	11.3	13.5	ns	-	-		
25 Jan.83	9.0	14.5	**	A,F,AxF	9.7	21.2	**
24 Feb.83	9.0	12.0	ns	AxF	12.7	22.2	***
9 Mar.83	13.6	17.1	ns	A	16.7	20.6	ns
7 Apr.83	18.7	25.1	ns	A,F,AxF	27.3	34.1	ns
4 May 83	11.7	12.5	ns	A	16.7	17.9	ns
14 Jun.83	8.8	13.9	*	-	-		
25 Jul.83	10.2	15.1	ns	A,F,AxF	10.9	25.8	***
7 Sep.83	7.2	12.8	**	A	9.9	15.3	**
12 Nov.83	7.2	8.6	ns	A	13.4	17.0	*
5 Jan.84	5.5	9.1	ns	F	4.9	2.9	ns
1 Mar.84	3.6	19.1	***	-	-		
11 May 84	5.2	18.4	***	-	-		
3 Aug.84	10.9	20.6	**	-	-		
24 Sep.84	6.1	16.9	**	-	-		
8 Jan.85	9.5	14.1	*	A	11.3	21.6	**

(See table 5 for explanation of column headings.)

Table 8. The accumulation, with leaf age, of proportion of foliar area covered by galls, calculated from the estimates for the discrete samples, averaged over all sampling occasions.

Age category	Total damage accumulated[1]			Rate of accumulation[2]	
	H	DB	t value[3]	H	DB
young	0.11±0.28(14)	.09±.21(15)	0.175 ns	.003	.003
nearly mature	0.49±0.83 (8)	.26±.36(10)	0.786 ns	.027	.012
mature	0.99±0.74(18)	.58±.42(17)	2.024 **	.002	.001
old	1.8 ±1.9 (20)	.91±.73(20)	1.916 **	.004	.002

[1] Calculated as the mean percentage of foliar area damaged, from all sampling occasions on which the age category was represented; recorded as mean ± std.dev. (number of sampling occasions)

[2] Calculated as the increment in total damage accumulated divided by the time span of each age category (table 1), expressed as % foliar area damaged per day.

[3] Calculated from data for damage accumulated on dieback and healthy trees; *** P<0.01, ** P<0.05, * P<0.10, ns P>0.10

Table 9. The accumulation, with leaf age, of proportion of foliar area which was necrotic, calculated from the estimates for the discrete samples, averaged over all sampling occasions.

Age category	Total damage accumulated			Rate of accumulation	
	H	DB	t value	H	DB
young	2.6±5.4(14)	2.7±5.6(15)	0.049 ns	.067	.083
nearly mature	2.9±2.6 (8)	4.3±5.9(10)	0.593 ns	.021	.109
mature	4.6±3.3(18)	4.6±4.1(17)	0.024 ns	.008	.001
old	7.9±3.4(20)	7.4±4.2(20)	0.414 ns	.015	.013

(See table 8 for explanation of column headings.)

Table 10. The accumulation, with leaf age, of proportion of foliar area removed, calculated from the estimates for the discrete samples, averaged over all sampling occasions.

Age category	Total damage accumulated			Rate of accumulation	
	H	DB	t value	H	DB
young	7.3±7.8(14)	7.1±6.0(15)	0.074 ns	.187	.215
nearly mature	11.0±6.4 (8)	12.7±5.1(10)	0.591 ns	.265	.400
mature	11.3±5.6(18)	16.5±3.8(17)	3.154***	.001	.015
old	13.1±6.1(20)	19.6±7.1(20)	3.111***	.008	.015

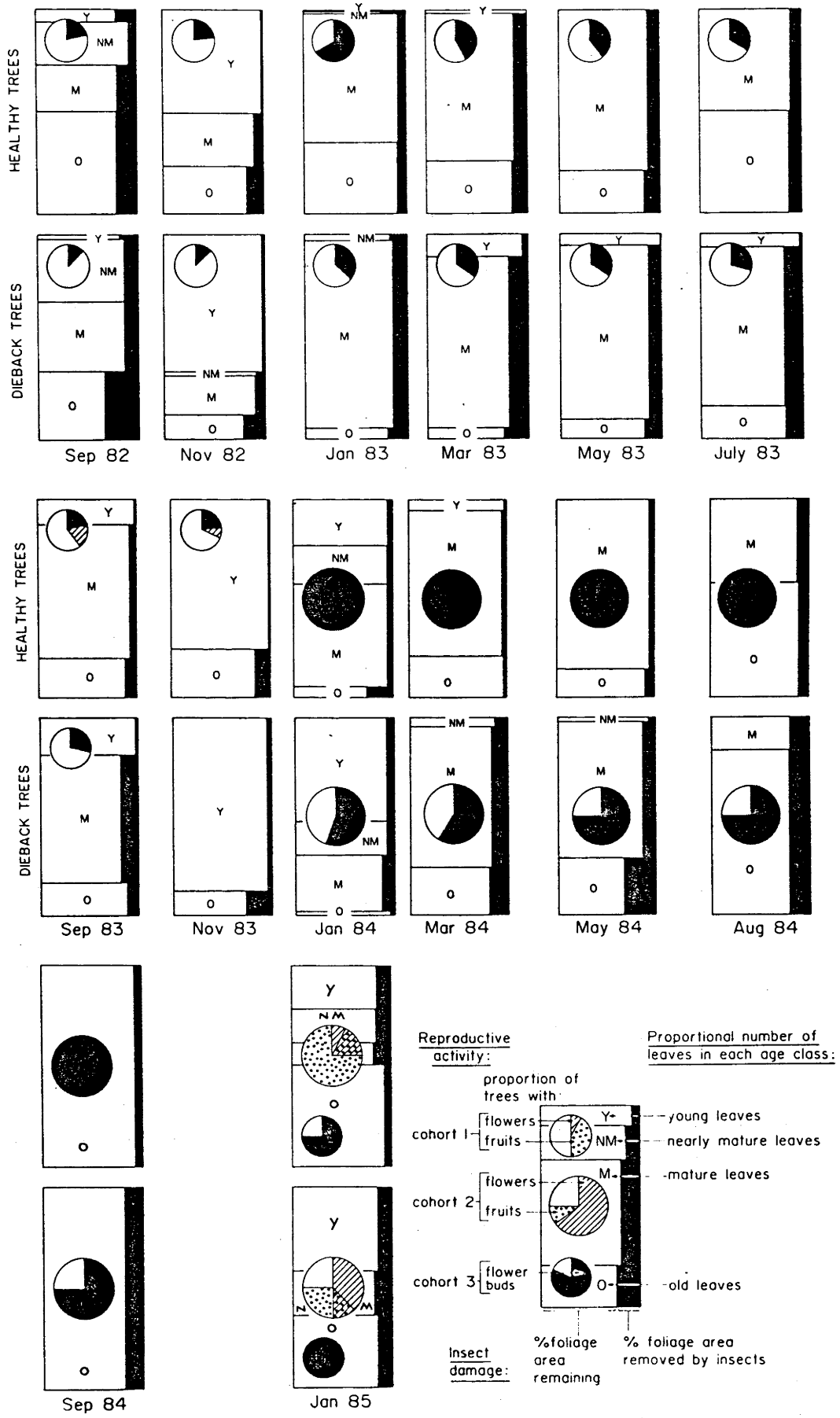
(See table 8 for explanation of column headings.)

Table 11. Insect species collected at the sites.

Order	Family	Genus and species	Feeding habits	Time collected
Coleoptera	Scarabaeidae	Anoplognathus pallidicollis (Blanchard)	leaf-chewing adults	December
		Anoplognathus pindarus (Carne)	leaf-chewing adults	December
		Anoplognathus sp. 3	leaf-chewing adults	December
		Liparetrus sp.1	leaf-chewing adults	April
		Liparetrus sp.2	leaf-chewing adults	April
		Automolius sp.1	leaf-chewing adults	April
		Automolius sp.2	leaf-chewing adults	February
	Chrysomelidae	Chrysophtharta sp.1	leaf-chewing adults	September
		Chrysophtharta sp.2	leaf-chewing adults	December
		Chrysophtharta sp.?	gregarious leaf-chewing larvae	December
		Paropsis atomaria (Oliver)	leaf-chewing adults	Sep.-Jan.
			gregarious leaf-chewing larvae	December
		Trachymela sp.	leaf-chewing adults	Sep.-Jan.
		Paropsisterna beata (Newman)	leaf-chewing adults	Jan. & Mar.
		Paropsisterna sp.?	gregarious leaf-chewing larvae	December
		Edusella sp.1	leaf-chewing adult	Nov.-Jan.
		Edusella sp.2	leaf-chewing adults	December
		Cryptocephalus haematodes (Boisduval)	leaf-chewing adults	December
		Brachycaulus ferrugineus (Fairmaire)	leaf-chewing adults	February
		Elaphodes pilula (Chapuis)	leaf-chewing adults	February
	Belidae	Isacantha sp.	leaf-chewing ? adults	November
	Curculionidae	Gonipterus scutellatus (Gyllenhal)	gregarious leaf-mining larvae	November
			leaf-chewing adults	Dec.-Jan.
Lepidoptera	Geometridae	Plesanemma fucata (Felder & Rogenhofer)	leaf-chewing larvae	September
	Anthelidae	Anthela varia (Walker)	leaf-chewing larvae	March
	Limacodidae	Doratifera oxleyi (Newman)	leaf-chewing larvae	October
	Nolidae	Uraba lugens (Walker)	gregarious leaf-skeletonizing larvae	Sep. & Oct.
	Noctuidae	?	leaf-chewing larvae	October
		?	leaf-chewing larvae	October
	Tortricidae	?	leaf-chewing leaf-binding larvae	November
	Psychidae	?	leaf-chewing case-building larvae	October

Hymenoptera	Pergidae	Perga affinis (Kirby)	gregarious leaf-chewing larvae	August
		Phylacteophaga eucalypti (Froggatt)	leaf-mining larvae	April
	Braconidae	Bracon sp.	parasite of above	April
	Eulophidae	Ophelimus sp.	gall-forming?	April
Hemiptera	Spondyliaspididae	Cardiaspina densitexta (Taylor)	sap-sucking nymphs in tests on leaves	Oct.-Mar.
		Glycaspis sp.	sap-sucking nymphs in tests on leaves	Oct.-Mar.
	Coccoidea	Eriococcus sp.	sap-sucking scale insects on leaves, petioles & stems	
	Flatidae	Siphanta sp.	sap-sucking adults	March
	Eurymelidae	Eurymeloides pulchra (Signoret)	sap-sucking nymphs & adults on petioles & stems	Nov.-Jan.

Figure 1. Seasonal changes, for the groups of discretely sampled dieback and healthy trees, in reproductive activity, in the relative numbers of leaves in different age classes, and in the proportion of foliar area damaged in each age class. The vertical axes of the bar graphs represent the numbers of leaves in each age class as a proportion of the total number sampled (Y = Young, NM = Nearly mature, M = Mature, O = Old). The horizontal axes represent the proportion of the foliar area in each age class which had been removed by insects (shaded = removed area, unshaded = area remaining). The pi graphs show reproductive activity. There were three age cohorts of flower buds, which emerged during January each year. Cohort 2 (larger circle) consisted of many more buds per tree. The shaded portions of each circle represent the proportion of trees, relative to the number sampled, which carried flower buds (shaded), flowers (cross-hatched), or fruits (stipled).


HEALTHY TREES
DIEBACK TREES
Y
NM
M
O
Sep 82
Nov 82
Jan 83
Mar 83
May 83
July 83
Sep 83
Nov 83
Jan 84
Mar 84
May 84
Aug 84
Sep 84
Jan 85
Reproductive activity:
proportion of trees with
cohort 1
flowers
fruits
cohort 2
flowers
fruits
cohort 3
flower buds
Proportional number of leaves in each age class:
young leaves
nearly mature leaves
mature leaves
old leaves
Insect damage:
%foliage area remaining
% foliage area removed by insects

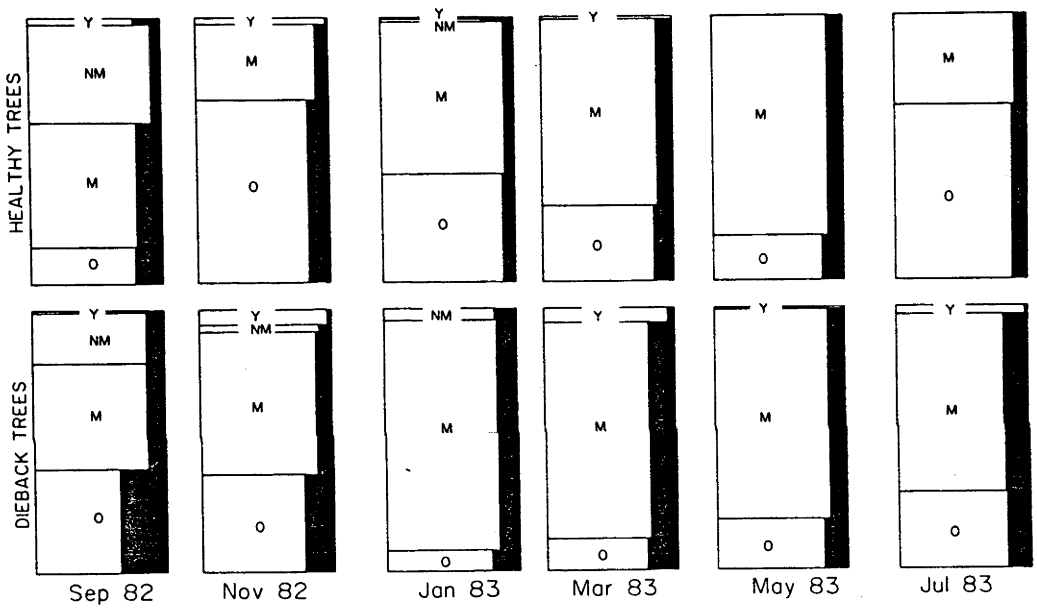


Figure 2. Seasonal changes, for the groups of discretely sampled dieback and healthy trees, in the proportion of foliar area in different age classes, and in the proportion of foliar area damaged in each age class. The vertical axes of the bar graphs represent the area of foliage in each age class as a proportion of the total area of foliage sampled. Annotations and horizontal axes as in figure 1.

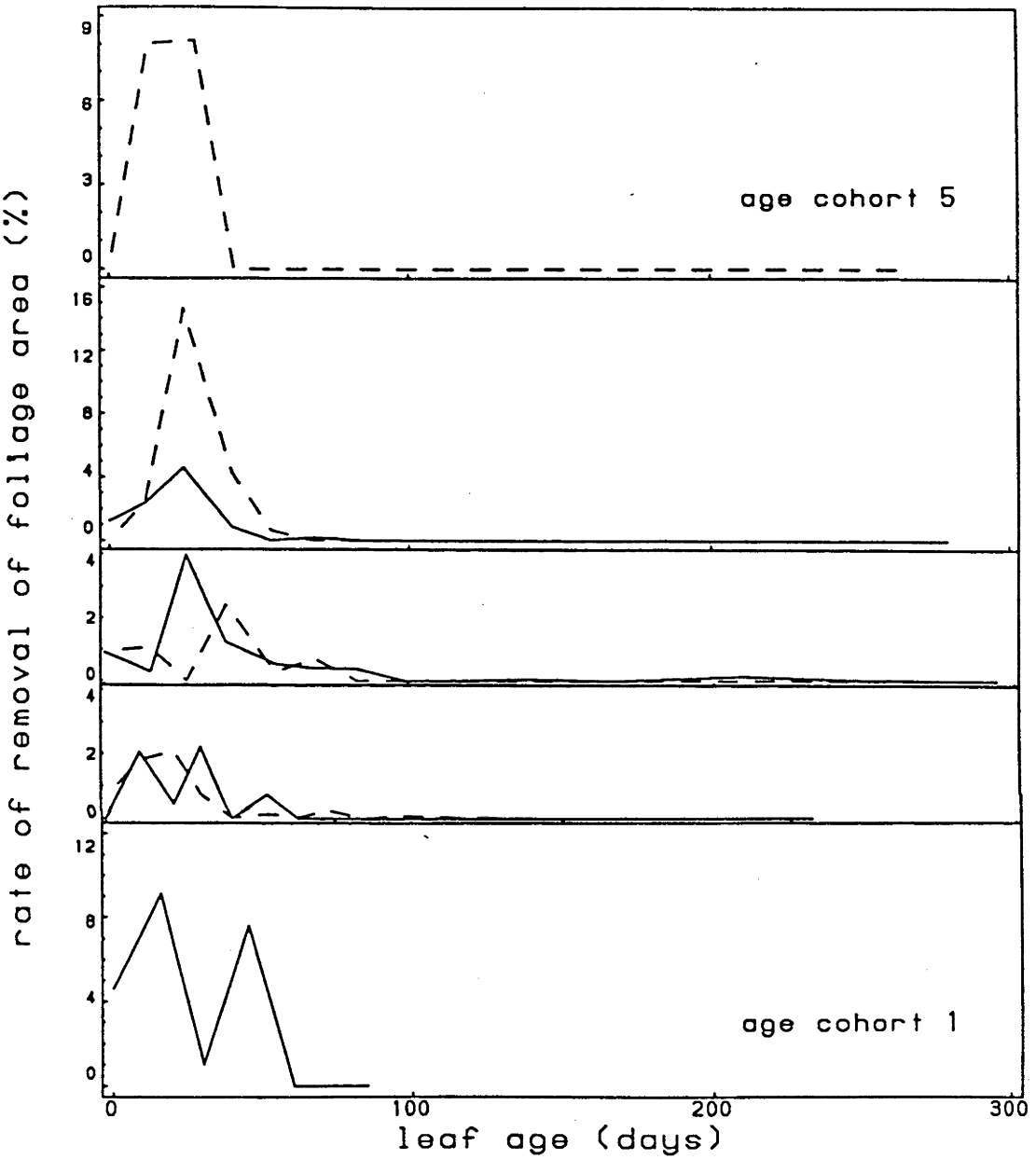
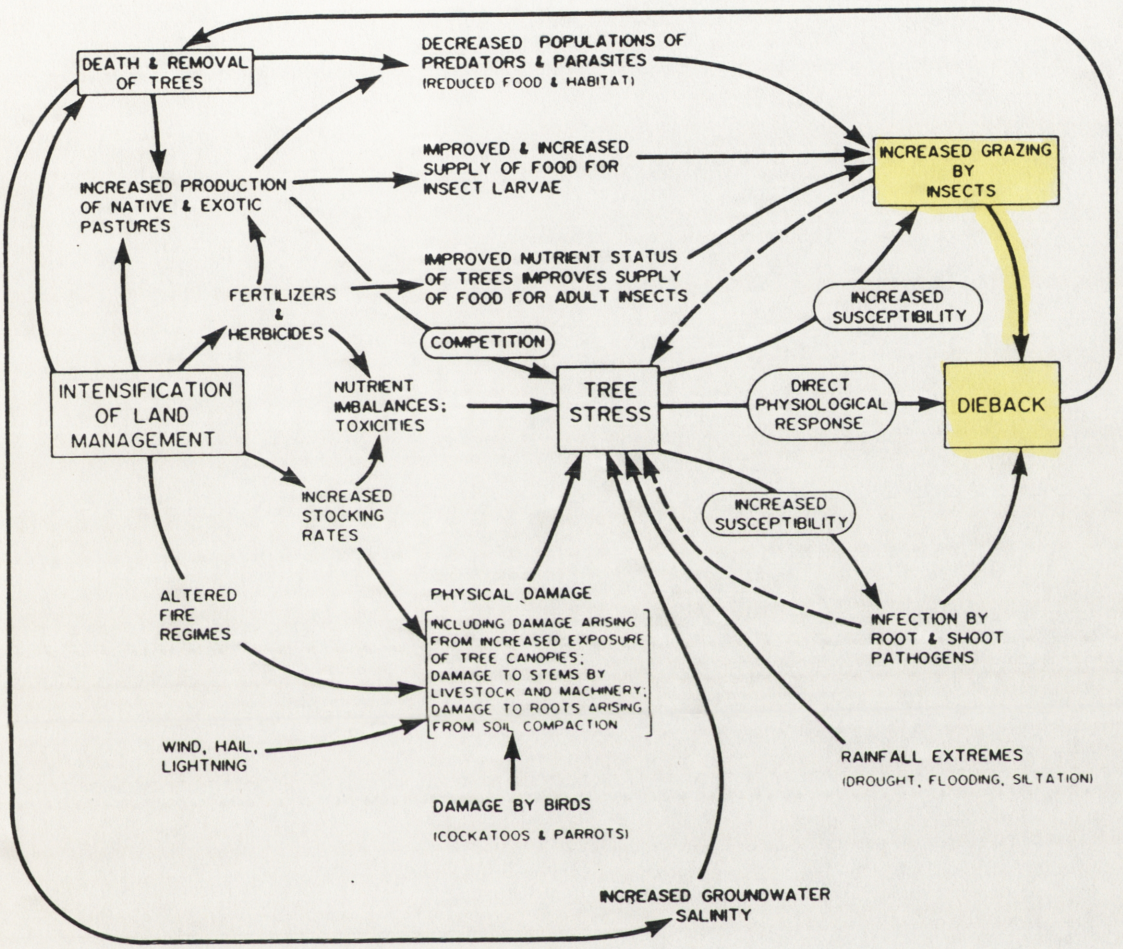
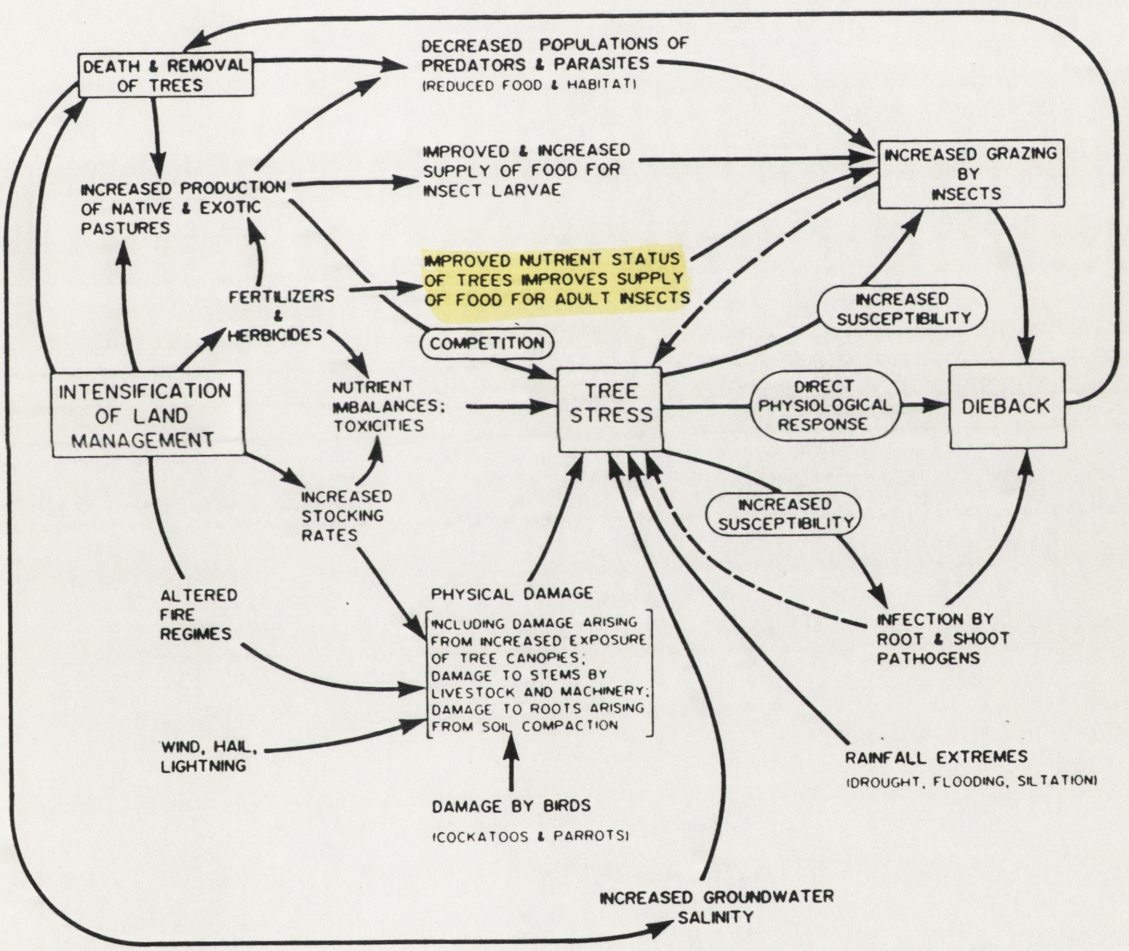


Figure 3. The rate of removal of foliar area from age cohorts of leaves, as they age. Solid lines represent cohorts on healthy trees; dashed lines represent cohorts on dieback trees. Areas of leaves whose total area was lost are not included.



On pastoral properties in the Australian Capital Territory, E. blakelyi trees with dieback are more heavily grazed by insects than are healthy trees growing nearby.

How does the dietary quality of the foliage of dieback trees compare with that of healthy trees?



SEASONAL VARIATION IN INSECT HERBIVORY RELATED TO THE DIETARY QUALITY OF THE FOLIAGE OF HEAVILY AND LIGHTLY GRAZED EUCALYPT TREES

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ABSTRACT

Foliar dietary quality, and the damage that insects caused to the foliage of dieback-affected and healthy Eucalyptus blakelyi trees, were monitored for three growing seasons, on pastoral properties in the Australian Capital Territory. The first season included a severe drought. Compared with healthy trees' foliage, the foliage of dieback trees was more heavily grazed by insects, and its dietary quality was generally superior. Some of the differences in dietary quality reflected differences in the average age of the foliage of healthy and dieback trees. But when statistical models were used to equalize the effects of differences in tree phenology, leaves on dieback trees still tended to contain more water and nitrogen, and to be rounder and to have lower specific weights. Drought caused deterioration in dietary quality of foliage, and foliage on drought-stressed trees was less damaged by insects. Many of the dietary quality variables were correlated with each other. Multiple regression equations incorporating seasonal means of several quality variables explained a high proportion of the variance in seasonal herbivory, but were grossly different between years. Separate regression analyses for each of the quality variables showed that there was a consistent significant relationship between herbivory and foliar nitrogen for both dieback and healthy trees, but that regressions between herbivory and specific leaf weight, shape, or sugar content were only consistently significant amongst the dieback trees. I interpreted this as an indication that these relationships may have been a response to, rather than a primary cause of, the repeated high defoliation of the dieback trees. These analyses illustrate some of the difficulties of moving from correlations between herbivory and dietary quality data to explanation of relationships or prediction. They also demonstrate the need for caution in formulation generalizations from limited seasonal data.

INTRODUCTION

The extent of the grazing damage caused by insects to eucalypt trees in Australia is highly variable, even amongst trees of the same species growing in similar environments (Fox & Morrow 1983). This variability is often accentuated for native trees growing on farms where much of the original forest or woodland vegetation has been cleared. Dieback of such trees is becoming increasingly common, and is often associated with heavy damage caused by grazing insects (Kile 1981). Where this occurs the dieback is often patchy, rather than extensive: trees with severe dieback are commonly found growing adjacent to healthy trees which appear, in other respects, very similar to the trees with dieback (Landsberg & Wylie 1983; Mackay *et al*. 1984).

Eucalypt blakelyi Maiden, a common tree species in the pastoral regions of the tablelands of south eastern Australia, is very susceptible to heavy insect grazing (Journet 1981), and to rural tree dieback (Duggin 1981). On pastoral properties in the Australian Capital Territory, I found that dieback-affected *E. blakelyi* trees usually sustained significantly more insect damage to their foliage than did healthy *E. blakelyi* trees growing nearby (Landsberg submitted b). This was partly because the foliage of the dieback trees tended to be younger, and was therefore more susceptible to insect grazing. In addition, however, foliage on dieback trees sustained more damage than foliage of similar age on healthy trees (Landsberg submitted b). I suspected that the most likely cause of these differences was variation in the dietary quality of the trees' foliage.

The quality of the diet of herbivorous insects is enhanced by high contents of water (e.g. Scriber 1977), nitrogen (e.g. Mattson 1980; McNeill & Southwood 1978), and sugars (e.g. Chippendale & Reddy 1974; Wensler & Dudzinski 1972). It is reduced by leaf toughness and high contents of lignin and fibre (e.g. Feeny 1970; Swain 1979), which may be associated with increasing specific weight of leaves (e.g. Waring *et al*. 1985). Insects tend to eat a greater area of thin, low specific weight leaves than of thicker leaves with higher specific leaf weights (e.g. Cooke *et al*. 1984). Secondary compounds, such as tannins and essential oils, appear to have a more variable effect on

the fitness of insects feeding on them (e.g. Bernays 1981; Morrow & Fox 1980). Although these relationships between dietary quality and insect fitness are well established, they have mostly been derived from laboratory-based studies (e.g. Fox & Macauley 1977; Ohmart et al. 1985 a & b; Scriber & Slansky 1981).

Surprisingly few field studies have investigated how well the dietary properties of leaves correlate with patterns of herbivory under natural conditions, and the results of these have been equivocal. For example Feeny (1970) proposed that the numbers of insects feeding on oak tree foliage decline as the foliage matures during its growing season because increasing maturity is associated with declining protein content of the foliage, and increasing tannin content and leaf toughness. Faeth (1985) however, found that tannin and protein content of oak foliage explained little of the variation in herbivory which he measured in oak trees, either during a growing season or between seasons. Coley (1983) investigated the extent to which dietary quality explained variations in herbivory between rain forest trees. She found that dietary quality, particularly leaf toughness, fibre content and nutrient value, explained much of the variation in herbivory between mature leaves of different tree species, but none of the variation in grazing damage on young leaves on the same plants.

Many of the leaf properties associated with dietary quality are highly correlated with each other (e.g. Coley 1983), and with leaf age and growing season (e.g. Raupp & Denno 1983). Many of them may also change following herbivory (e.g. Ericsson et al. 1985; Heichel & Turner 1976; Valentine et al. 1983). This interdependence poses major problems of interpretation, especially when statistical techniques such as multiple regression analysis are used to attempt to explain variation in herbivory in terms of dietary quality covariates.

I monitored dietary quality and insect damage of foliage from dieback-affected and healthy E. blakelyi trees for three growing seasons. From these data I determined whether differences in the amount of insect damage that dieback and healthy trees sustained were correlated with the dietary quality of their foliage. I also investigated the way in which correlations were dependent on

differences between the trees in the average age of their foliage. Because the first growing season of my study included several months of severe drought, I was also able to determine how this influenced both dietary quality and herbivory. In addition I investigated regression relationships between the damage sustained by individual trees during each season, and the seasonal mean values of their foliage dietary quality. I did this for each of the dietary quality variables separately, and for various combinations of them, to determine how much of the variation in levels of defoliation could be explained in terms of the dietary quality variables I measured.

METHODS

STUDY SITES AND TREES

I studied mature *E. blakelyi* trees (average height 10-12 m) growing on two pastoral properties near Hall in the Australian Capital Territory, from September 1982 to January 1985. The properties are managed for grazing of sheep and cattle, and the trees, whose apparent health varies markedly, are remnants of the original natural woodland retained for shade and shelter. I classified them as 'healthy' or 'dieback' from an assessment of the size and density of their crowns and the extent of epicormic growth and branch death; the foliage of the dieback trees was generally more heavily grazed by insects (Landsberg submitted b). I sampled twenty trees (five healthy and five dieback at each site) at about monthly intervals for the first year, and 16 trees at one site only at less regular intervals for the rest of the study. (These comprised the original 10 trees, plus an additional three healthy and three dieback trees).

One of the most severe droughts the region has experienced ended in late March 1983 and the months following varied from 'near normal' to 'very wet' (McDonald 1984). Several trees showed some symptoms of drought stress before the drought broke, but all had apparently recovered by the following growing season (Landsberg 1985). *E. blakelyi* trees tend to have a two year cycle of reproduction and

foliage replacement (Clark & Dallwitz 1974). During this study most new leaves were initiated between late spring and mid-summer (November to January), and leaves tended to remain on the trees for about 18 months (Landsberg submitted b). A major leaf flush (about three quarters of each foliage sample consisted of young leaves) occurred in November 1983, and minor leaf flushes occurred during November-December 1982, and during the 1984-5 growing season.

HERBIVORY AND DIETARY QUALITY

The extent of damage caused by insects, and foliar dietary quality, were assessed on foliage samples of about 100 leaves per tree. These were cut from study trees before dawn and stored in black plastic bags in an ice box until they could be processed, which was completed by three to four hours after cutting. This procedure minimized variation in dietary quality due to diurnal fluctuations and sample handling. Processing consisted of sorting leaves from each tree into age (young, nearly mature, mature 1, mature 2, old 1 and old 2) and form (epicormic, intermediate 1-3, and adult) categories, based on their appearance and their pattern of emergence along shoots and branches. A hole punch was used to cut a subsample of known area from undamaged portions of leaves in each foliage category, and the leaf discs were stored in pre-weighed vials under liquid nitrogen for transport to the laboratory. There they were weighed, lyophilized, reweighed, and ground to a fine powder. Ground samples were stored at $-15^{\circ}C$ in vials above a desiccant until they could be analyzed, up to nine months later.

The foliage samples from which discs were cut were dried in separate folders in plant presses. The amount (% foliar area) of grazing damage caused by insects to these samples was estimated visually into nominal classes (none, a little, about an eighth, etc.), which were later calibrated against instrumented measurements (Landsberg submitted a).

The dietary quality variables measured were:

Water content, from (leaf fresh weight - freeze dried weight) / fresh weight x 100%

Specific leaf weight, from (freeze dried weight) / (area of a leaf disc x number of discs)

Shape, from a standard form factor (4π x area / perimeter^2) calculated from measurements made by tracing estimated original outlines of a subset of 20 leaves in each age/form/tree category, on a digitizing board connected to a desk-top microcomputer. The form factor tends from 1.0 for a circle towards zero as the shape becomes more elongate.

Total nitrogen content (% dry weight), which was measured using a Technicon autoanalyzer, following micro-Kjeldahl digestion.

Soluble sugar content (% dry weight), which was measured using an enzyme method, following extraction in boiling water. Sucrose was hydrolyzed to glucose and fructose by incubation with invertase (Sigma 1-4504), fructose was converted to glucose with isomerase (Sigma R5381), and the glucose in the final solution was measured in an assay using a glucose-specific reagent (Calbiochem-Behring s.v.r. 870104) (Azcon-Bieto & Osmond 1983).

Tannin content (% dry weight), which was estimated from relative astringency of a methanol/water extract compared with a tannic acid standard, by precipitation of haemoglobin from a centrifuged and filtered solution of fresh sheep's blood and iced water (Schultz et al. 1981).

Essential oil content (% dry weight), which was determined by gas chromatography of a chloroform extract containing 1µl.ml^{-1} n-dodecane as an internal standard. Extraction was conducted in flame-sealed glass vials containing sample and extractant. These were heated in a boiling water bath for 30 minutes, after which time extraction was complete. Gas chromatography was by injection onto glass columns (183 cm long x 0.64 cm i.d.) packed with 5% OV-101. Carrier gas was nitrogen, and the column was heated from 40°C to 180°C at 4° min^{-1}.

Measurements of specific leaf weight, water content and nitrogen were made on all samples collected. Tannins and soluble sugars were measured on samples collected till autumn 1984 only, and shape at less frequent intervals during that time. Essential oils were only measured on leaves collected during the 1983-4 summer.

RESULTS

COMPARISON OF DIEBACK AND HEALTHY TREES

From the data from each sampling date I tested the significance of differences between the dieback and healthy trees in the mean values of each of the dietary quality variables measured, by analysis of variance. I calculated two sets of mean values. 'Unadjusted means' (Tables 1 & 3) were calculated from mean values for the samples from each tree, regardless of the age and form categories represented, and 'adjusted means' (Tables 1 & 3) were calculated from fitted statistical models. These adjusted the mean values to account for any significant variation amongst the trees which resulted from the effects of differences in the age or form of their leaves, or interactions between these and the health of the trees ('significant model terms' in table 2) (see Landsberg submitted b for a description of the technique).

In general, leaves from dieback trees tended to contain more water and nitrogen, and to be rounder and have lower specific weights, than leaves from healthy trees. They also tended to sustain more damage from insects (Tables 1 & 3; 'unadj.'). Variation in age and form of foliage contributed to many of these differences (Table 2). However, when means were adjusted to equalize these effects, the same trends were maintained, although the significance of the differences in water content was usually decreased (Tables 1 & 3; 'adj.'). The contents of sugar, tannin and essential oils were similar in foliage from both dieback and healthy trees, both before and after adjustment. On the only occasion when differences in sugar content were significant the

dieback trees' foliage contained less, and on the only occasion when tannin differences were significant, foliage from the dieback trees contained more.

THE INFLUENCE OF PHENOLOGY

Leaf age contributed to differences between trees in their foliar properties more often than did leaf form or any of the interactions tested (Table 2). In general, foliage from dieback trees tended to be younger than foliage from healthy trees (Landsberg submitted b). Many of the differences between younger and older foliage paralleled differences between foliage of similar age from dieback and healthy trees. Young foliage and foliage from dieback trees each tended to contain more water and nitrogen, less essential oil, and to have lower specific leaf weights than either older foliage or the healthy trees' foliage, respectively (Table 4). Thus for these properties, differences in the average age of the trees' foliage tended to reinforce intrinsic differences apparent in foliage of similar age from both dieback and healthy trees.

In contrast, the tannin content of foliage tended to decrease, and leaves tended to become rounder, and to accumulate more damage as they aged. These trends were opposite in direction to intrinsic differences between foliage from dieback and healthy trees (Table 4). The difference in average age of foliage from dieback and healthy trees tended to negate intrinsic differences in their tannin content; this is probably why differences between trees were seldom significant for foliar tannin (Table 1). However, the effect of age on leaf shape must have been outweighed by intrinsic differences, since differences in leaf shape were still significant at the whole tree level. Damage is a cumulative measure. Thus damage measured on older leaves includes damage sustained when the leaves were younger. The rate at which young leaves were damaged was much higher than the rate at which older leaves were damaged (Landsberg submitted b). Therefore intrinsic differences in rate of damage by insects and in foliar age structure both tended to favour higher damage on dieback trees.

Young leaves from dieback trees contained significantly less sugar than young leaves from the healthy trees, though differences between older leaves were not significant (Table 4). This is probably why the foliage from the dieback trees contained less sugar in January 1984 (Tables 1 & 3), when much of the foliage of trees at the study sites was young (Landsberg submitted b).

THE INFLUENCE OF DROUGHT

Only four of the study trees showed obvious visual symptoms of drought stress (some leaf chlorosis and premature shedding of older leaves), and these had the lowest predawn water potentials at the peak of the drought, in March 1983. All were at the same site and two had been earlier classified as 'healthy' and two as 'dieback'. Despite the symptoms of drought stress the relative differences in their canopy appearance were retained. The other six trees (3 healthy and 3 dieback) at this site showed little effect of the drought. A year after the drought had broken (March 1984) all the trees at the site had largely replaced their canopies with an abundance of new growth produced in late spring, although again the relative differences in appearance of dieback and healthy trees were retained (Landsberg 1985).

Dietary quality and herbivory of foliage of the four drought-stressed trees were compared with those of the other six trees at the same site, both at the peak of the drought and one year later, using the same statistical model procedure and analysis of variance (in this case tree health x water status) of mean values per tree as described earlier.

At the peak of the drought the foliage of the drought-stressed trees had significantly less water, less nitrogen, more tannin and higher specific leaf weights than the foliage of the trees which showed no symptoms of drought stress (Table 5). This comparison is remarkably similar to that between dieback and healthy trees, except that the dietary quality of the foliage of the drought-stressed trees is more similar to that of healthy, rather than dieback, trees.

A year after the drought had broken the dietary quality of the foliage of the trees which had been stressed by the drought was no longer significantly different from that of the trees which had not shown signs of drought stress. Differences in herbivory levels, however, were significant, and followed the same trend as at the peak of the drought: the foliage of the trees which had been drought stressed and the foliage of the healthy trees was less damaged by insects (Table 5).

RELATIONSHIPS BETWEEN DIETARY QUALITY VARIABLES AND HERBIVORY

Since dietary quality variables are relatively labile, but the extent of herbivory accumulates with increasing leaf age, regressions between the quality variables and herbivory on each sampling occasion would not be very meaningful. Instead, for each tree, average values for the quality variables were calculated over a whole growing season, and these were compared with the herbivory accumulated during that season.

Analyses were restricted to only those leaves produced during each growing season (September 1982 to September 1983 or September 1983 to September 1984). 'Seasonal means' were calculated for each of the quality variables for each tree (except for essential oils, which were measured on only two occasions), from all the samples collected from that tree during that season. 'Seasonal herbivory' was measured as the proportion of foliar area removed from foliage samples collected from each tree at the end of the season.

The data for 1982-3 (Fig.1A) relate to 19 trees. Measurements were made on 20 trees, but the seasonal herbivory measurement for one dieback tree was abnormally high. In September 1983 the damage measure for this tree was 36.7%, compared with a mean value for the other dieback trees of 14.7%. On all preceding sampling occasions the value for this tree had been less than the mean of the values for the other dieback trees. Most of the additional damage to this tree's September sample had been made on only eighteen of the 100 leaves in the sample, by gum leaf skeletonizer (Uraba lugens Walk.) larvae, which are gregarious feeders. Since this damage was judged to be

atypical of the whole tree, this tree was excluded from the analyses. The data for 1983-4 (Fig.1B) relate to only 10 trees (six additional trees were sampled during 1983-4, but not till after the main growth flush was finished), and are incomplete, in that late season concentrations of tannins and soluble sugars were not measured.

'Healthy' and 'dieback' represented two levels of a factor describing tree health. This factor could influence relationships between seasonal herbivory and seasonal means of the dietary quality variables in three basic ways:

1. A relationship could be independent of tree health, i.e. the slope and intercept of a regression relating herbivory and a dietary quality variable could be the same for dieback and healthy trees (Tables 6 & 7 regression A). Such a relationship would indicate that herbivory and the quality variable were directly related, regardless of the health of the trees. However, this relationship was not the most appropriate for any of the quality variables measured (Tables 6 & 7). Thus none of these quality variables is likely to be a direct, dominant cause (or consequence) of herbivory. Instead, relationships are dependent to some extent on trees' health, and, by extension, their previous defoliation history.

2. The proportionality between herbivory and a quality variable could be the same for both healthy and dieback trees, although their actual herbivory levels could differ (same slope, different intercept; Tables 6 & 7 regression B). This could occur if herbivory and a quality variable were directly related, but this relationship were insufficient to explain some underlying difference in herbivory levels between the groups of trees. This type of regression was the most appropriate for several of the dietary quality variables I measured (Tables 6 & 7). However, the slope of the regressions for water content in the first year, and for shape in the second year, did not differ significantly from zero (t tests). Thus although the mean values of herbivory and these quality variables differed between dieback and healthy trees, there was no significant regression within either group of trees between herbivory and either of the quality variables. In contrast, the slope of the regression between herbivory and nitrogen content was significantly greater than zero in both

years. Thus herbivory and foliar nitrogen were positively related for both dieback and healthy trees, although this relationship did not account for an intrinsically higher level of herbivory on the dieback trees.

3. Both the proportionality and the actual levels of herbivory could differ for both healthy and dieback trees (different slopes and intercepts; Tables 6 & 7 regression C). For each of the instances in my study where this was the most appropriate relationship (Tables 6 & 7), the slope of the regression for the healthy trees did not differ significantly from zero (t tests). This was the case for specific leaf weight, shape, sugars and tannin in the first year, and tannin in the second. Thus relationships between herbivory and many of the quality variables existed only amongst the dieback trees. (This was most marked during the first year of the study, when twice as many trees were measured.) For these relationships the regressions of the quality variables against herbivory were apparently dependent on some aspect of the dieback condition of the trees, such as high levels of defoliation during the current growing season, a history of repeated defoliations, or some other factor associated with low tree vitality.

Only the regressions for specific leaf weight, sugar, nitrogen and tannins had non-zero slopes in both years. The direction of the relationships were consistent for all but tannin content, which was positive in the first year and negative in the second. The biological relevance of these tannin regressions is therefore questionable.

Many of the dietary quality variables were correlated with each other (Tables 8 & 9; correlation coefficients are presented for the dieback trees only, since the quality variables were seldom related to herbivory for the healthy trees). However, only two of the correlations were consistent in for both years, a positive correlation between sugar content and specific leaf weight, and a negative correlation between nitrogen and tannin content.

Partial correlation coefficients were calculated for some of these relationships (Table 10), to determine if any of the correlations between herbivory and a quality variable were improved when the value of a second, intercorrelated quality variable was held constant

(Snedecor & Cochran 1980). However, none of the partial correlations calculated consistently improved the significance of a relationship between a quality variable and herbivory in both years, and in several instances the partial correlations were less significant than the ordinary correlations. Thus it was not possible to identify a particular dominant correlation between herbivory and any one of the intercorrelated quality variables.

This degree of intercorrelation, and the relatively small size of the samples, meant that it would be difficult to interpret the results of multiple regression analyses in any causal sense (Snedecor & Cochran 1980). However multiple regression has often been used to relate herbivory to dietary quality in other studies (e.g. Coley 1983; Faeth 1985), and has the potential to provide predictive equations. Therefore, although recognizing their limitations, I fitted multiple regression equations to the data for the dieback trees, with herbivory as the dependent variable and the dietary quality variables as independent variables. For the 1982-3 data soluble sugars were entered as the first step, and accounted for 67% of the variance ($F=16.24$; $df=1,7$; $P<0.01$). When shape was added this increased to 89% of the variance ($F=14.79$; $df=1,6$; $P<0.01$), and adding nitrogen accounted for 96% of the variance in herbivory ($F=12.88$; $df=1,5$; $P<0.025$). The regression equation incorporating these three variables was:

herbivory = -17.6 - (5.6 x soluble sugars) + (0.4 x shape) + (20.0 x nitrogen)

Although this equation 'explained' a very high proportion of the variance in herbivory in 1982-3, it was totally ineffective in explaining any of the variance in herbivory in the following year. Multiple regression analysis for the 1983-4 data for dieback trees showed that only water content contributed significantly to the variance in herbivory ($F=5.97$; $df=1,3$; $P<0.10$; variance accounted for = 55%). The regression equation was:

herbivory = 164.7 - (2.58 x water content)

Thus not only was multiple regression inappropriate for disentangling any causal relationships between the dietary quality variables and herbivory, it was also unsuccessful in predicting relationships which were consistent between years.

DISCUSSION

As I had anticipated from my earlier studies, the foliage of dieback trees was more damaged by insects than was that of the healthy trees nearby. Furthermore, many of the differences in foliar properties of the trees were as predicted from theories of dietary quality: dieback trees' foliage tended to be more nutritious, at least in terms of high water and nitrogen contents and low specific leaf weights. It may also have been less well defended, at least in terms of intrinsic (age for age) differences in tannins and essential oils. The low soluble sugar contents of young foliage from dieback trees may have reduced its dietary quality, but differences in foliar sugar content were rarely significant at the whole tree level. The rounder shape of dieback trees' leaves may have had relatively little impact on the pattern of feeding by insects. Carne (1965), for example, found that although female sawfly (Perga affinis affinis) adults preferred to oviposit on narrow E. blakelyi leaves, migrations by the larvae often resulted in grazing damage becoming independent of leaf shape.

The younger age of dieback trees' foliage tended to reinforce most of those characteristics that enhanced its dietary quality (high water and nitrogen contents, and low specific leaf weight), though it also tended to negate any beneficial influence its relatively low intrinsic concentration of tannin may have had.

In contrast to the pattern I measured, of highest tannin concentration in young foliage, early research on tannins in foliage showed a pattern of increasing tannin concentration with leaf age (e.g. Feeny 1970 with oak trees; Dement & Mooney 1974 with an evergreen shrub; Lawton 1976 with bracken fern). Although Macauley and Fox (1980) showed that the foliar tannin content of several

species of eucalypts did not follow this trend, it was believed to be generally true of most other plants and was incorporated into several theories of plant-herbivore interactions (e.g. Feeny 1976; Rhoades & Cates 1976; Scriber & Slansky 1981). However more recent work (e.g. Schultz et al. 1982 with maple and birch trees; Faeth 1985, also with oak trees) has shown more variable patterns of seasonal changes in tannins, and Coley (1983; rainforest trees), Cork and Pahl (1984; eucalypts), Prudhomme (1983; subarctic shrubs), and Puttick (1986; Californian oak trees) have also measured highest concentrations of tannins and phenolics in young leaves. Part of the reason for these differences may be the different assay methods used (e.g. see Becker & Martin 1982), but the pattern described here for E. blakelyi trees may also be more common than previously suspected.

The way in which drought stress influenced foliar properties is of interest for two reasons. Firstly it was opposite in direction to changes predicted by a substantial body of theory. Mattson and Addy (1975), for example, reviewed many instances of trees under stress becoming more susceptible to herbivory. White (1974, 1976, 1984), and Rhoades (1983) have proposed that this increase in susceptibility occurs because of changes in foliar dietary quality. White suggested that the key factor is an increase in the amount of foliar nitrogen available to young insects, while Rhoades placed more importance on an imbalance between nutrition and plant defences such as tannins. However the most drought-stressed trees in my study became less, rather than more, susceptible to damage by insects. In partial support of White's hypothesis this decrease in susceptibility was associated with a decrease in nitrogen concentration, and in contradiction of Rhoade's hypothesis, it was also associated with a decrease in the concentration of foliar tannin. White (1984) has suggested that more extreme forms of stress, sufficient to cause severe wilting or scorching of plants, may cause foliage deterioration, and may thus have an opposite effect to milder forms of stress. Thus a possible explanation of my results is that the drought stress experienced by the trees in my sample was extreme. However, this did not appear to be so. The trees I studied did not become severely wilted or suffer very much leaf scorch, and they recovered quickly in the first growing season which followed the drought. From the state of their foliage they did not appear severely stressed,

either in comparison with populations of eucalypts in other districts during the same drought, or in comparison with populations of eucalypts in the same district during an earlier drought (Pook 1986).

The second point of interest concerning the influence of the drought on foliar properties is the similarity in foliar properties of the dieback-affected and the least stressed trees: in addition to incurring greater insect damage, the foliage from both groups of trees showed similar trends of high concentrations of water and nitrogen, and low specific leaf weights. Because there was no apparent correlation between the dieback and the drought stress (Landsberg 1985), this suggests that these dietary quality variables may be reasonable predictors of the susceptibility of foliage to insect herbivory under quite different circumstances.

However, probably because of the degree of interdependence between herbivory and the dietary quality variables, the results of multiple regression analyses were difficult to interpret biologically, and did not provide consistent predictions. Faeth (1985) also found that multiple regression equations of herbivory against dietary quality were grossly different between years, so this may be a general problem with these kinds of data.

Regressions of herbivory against a single quality variable, repeated for each of the quality variables separately, were more informative. The nature of the relationship between each quality variable and herbivory depended on tree health. The relationship between nitrogen and herbivory was similar for both dieback and healthy trees, but was not sufficient to explain intrinsically higher levels of defoliation on dieback trees. This could indicate that total nitrogen was not the best measure of the nitrogen requirements of insects, or that some other aspect of dietary quality is also involved in determining herbivory differences. Coley (1983), for example, found that fibre content and leaf toughness were highly correlated with herbivory, and I did not measure either of these. Alternatively, high levels of defoliation on dieback trees may result from some feedback effect of previous defoliations. For example, the predictability of finding foliage with favourable dietary quality may be much higher on trees that have been defoliated repeatedly.

The other consistent relationships between herbivory and a quality variable (specific leaf weight, sugars, and shape) were more likely to have arisen as a consequence of repeated high defoliation, rather than as a primary cause of it, since they were not apparent amongst the healthy trees. This conclusion is in agreement with other studies. Foliar sugar concentrations often decline following defoliations (e.g. Valentine et al. 1983), and the replacement epicormic foliage produced by eucalypts is usually rounder in shape (Jacobs 1955), and may also differ physiologically (e.g. Blake 1980). However, for specific leaf weight at least, a feedback process may also have operated. High defoliation may have initially caused the production of low specific weight foliage, but this property may also have enhanced its susceptibility to further herbivory. The low specific weight of replacement foliage could help trees to more quickly compensate for foliage lost to herbivores, because it results in a greater area of photosynthetic tissue being available per unit of leaf weight produced. However, if the leaf area consumed by herbivores also partly depends on their intake of biomass, then the benefit of increased photosynthetic capacity per unit area may also incur the cost of increased consumption per unit area by herbivores.

Thus although damage caused by grazing insects correlated well with the dietary quality of the foliage of heavily and lightly grazed trees in this study, the more detailed regression analyses I have presented illustrate some of the problems and pitfalls associated with untangling causal relationships from correlations such as these.

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Table 1. Significance of differences in foliage properties between dieback-affected and healthy trees.

Sampling date	F-values (ANOVA) [1] Water content unadj.	adj.	Nitrogen cont. unadj.	adj.	Sugar content unadj.	adj.	Specific weight unadj.	adj.	Tannin cont. unadj.	adj.	Shape unadj.	adj.	Insect damage [2] unadj.	adj.[3]
13 Sep 82	3.3^{*}	0.9^{ns}	1.3^{ns}	2.4^{ns}	0.0^{ns}	-	4.6^{*}	3.8^{*}	0.5^{ns}	9.2^{***}	. NM		1.5^{ns}	5.6^{**}
3 Oct 82	1.3^{ns}	0.9^{ns}	3.0^{*}	7.0^{**}	0.0^{ns}	2.0^{ns}	3.4^{*}	3.8^{*}	1.7^{ns}	0.7^{ns}	0.4^{ns}	0.2^{ns}	5.4^{**}	4.0^{**}
2 Nov 82	5.8^{ns}	0.1^{ns}	4.7^{**}	1.2^{ns}	0.0^{ns}	1.1^{ns}	13.7^{***}	7.1^{ns}	0.4^{ns}	2.4^{ns}	14.1^{***}	2.7^{ns}	0.2^{ns}	2.3^{ns}
2 Dec 82	3.4^{*}	0.6^{ns}	5.6^{**}	11.3^{***}	0.9^{ns}	-	6.3^{**}	0.3^{ns}	0.0^{ns}	0.3^{ns}	. NM		0.1^{ns}	1.4^{s}
27 Dec 82	1.0^{ns}	0.1^{ns}	9.0^{***}	2.2^{ns}	0.0^{ns}	2.8^{ns}	2.4^{ns}	0.7^{ns}	0.6^{ns}	0.0^{ns}	. NM		0.6^{s}	-
25 Jan 83	1.7^{ns}	-	5.7^{**}	-	0.1^{ns}	-	9.2^{***}	-	0.3^{ns}	-	1.8^{ns}	-	5.5^{*}	5.3^{*}
24 Feb 83	2.3^{ns}	0.1^{ns}	5.8^{**}	-	2.7^{ns}	-	17.1^{***}	-	0.8^{ns}	0.1^{ns}	. NM		1.4^{ns}	18.1^{**}
9 Mar 83	5.8^{**}	30.1^{***}	4.9^{**}	-	1.1^{ns}	-	15.2^{***}	16.3^{***}	0.0^{ns}	0.1^{ns}	. NM		0.9^{s}	1.2^{ns}
7 Apr 83	6.5^{**}	0.3^{ns}	2.7^{ns}	4.3^{*}	1.9^{ns}	-	25.0^{***}	9.5^{***}	0.1^{ns}	-	1.7^{ns}	-	2.4^{ns}	1.8^{ns}
4 May 83	2.7^{ns}	1.5^{ns}	5.4^{**}	-	1.3^{ns}	-	13.7^{***}	-	2.0^{ns}	-	. NM		0.1^{s}	0.2^{s}
14 Jun 83	0.1^{ns}	0.2^{ns}	3.1^{*}	2.3^{ns}	0.1^{ns}	-	5.9^{**}	8.6^{***}	2.4^{ns}	-	. NM		3.9^{*}	-
25 Jul 83	2.0^{ns}	-	3.2^{*}	-	0.4^{ns}	-	13.0^{***}	-	0.8^{ns}	-	13.5^{***}	-	2.0^{ns}	8.8^{**}
7 Sep 83	1.8^{ns}	-	0.9^{ns}	-	1.4^{ns}	-	8.6^{***}	9.2^{***}	0.0^{ns}	-	. NM		5.4^{*}	5.8^{*}
12 Nov 83	5.9^{**}	0.5^{ns}	2.1^{ns}	0.3^{ns}	0.5^{ns}	-	11.3^{***}	17.3^{***}	0.1^{ns}	0.0^{ns}	60.2^{***}	20.9^{***}	0.3^{s}	4.6^{*}
5 Jan 84	2.0^{ns}	9.9^{**}	2.0^{ns}	-	26.1^{***}	25.2^{***}	9.8^{**}	8.8^{**}	0.1^{ns}	1.3^{ns}	15.7^{***}	33.3^{***}	3.3^{ns}	0.2^{s}
1 Mar 84	1.2^{ns}	2.1^{ns}	0.5^{ns}	-	0.8^{ns}	-	0.8^{ns}	-	0.0^{ns}	-	. NM		8.8^{***}	-
11 May 84	1.2^{ns}	-	0.1^{ns}	-	. NM		12.7^{***}	-	0.6^{ns}	-	. NM		11.0^{***}	-
3 Aug 84	0.3^{ns}	-	0.7^{ns}	-	. NM		8.9^{***}	-	. NM		. NM		5.6^{**}	-
24 Sep 84	1.6^{ns}	1.2^{ns}	0.1^{ns}	-	. NM		13.9^{***}	-	. NM		. NM		6.2^{*}	-
8 Jan 85	1.6^{ns}	0.1^{ns}	3.9^{*}	-	. NM		21.0^{***}	21.0^{***}	. NM		. NM		4.1	5.3^{*}

1. F-values calculated from analysis of variance for mean values for healthy and dieback trees. From 13 Sep 82 to 7 Sep 83 df = 1,16; for 12 Nov 83 & 5 Jan 84 df = 1,8; from 1 Mar 84 to 8 Jan 85 df = 1,14. ***p<0.01, **p<0.05, *p<0.10, ns p>0.10. NM indicates that no measurements were made for that date. Essential oil contents were measured on samples collected on 12 Nov 83 and 5 Jan 84, but differences between dieback and healthy trees were not significant (F<1.4).

2. Water content was measured as % fresh weight; nitrogen, sugar & tannin contents as % dry weight; specific weight as $mg.cm^{-2}$; insect damage as the % of foliage area removed by insects; shape varied from 1(=spherical) to 0.

3. Unadjusted mean values ('unadj.') were not adjusted for any differences in leaf age or form. Adjusted mean values ('adj.') were calculated by fitting regressions for each tree, incorporating the model terms shown in Table 2. Thus means were adjusted to equalize the effects of these terms for between tree comparisons. Dashes indicate that adjusted means were equivalent to unadjusted means (no significant model terms; Table 2).

Table 2. Factors related to tree phenology that significantly contributed to within-tree variation in foliage properties. These were incorporated as terms in the statistical models from which adjusted means (Tables 1 & 3) were calculated.

Sampling date	Significant model terms: Water content	Nitrogen content	Sugar content	Specific weight	Tannin content	Shape	Insect damage
13 Sep 82	A	F	-	A,F	F	NM	A
3 Oct 82	A,F	A,F,FxH	A,AxF	A,F,AxH,FxH	A	A,F,AxF,AxH	A
2 Nov 82	A	A	A	A	A,F,AxF	F	A,F,AxF
2 Dec 82	A	A	-	A,F,AxF	A	NM	A
27 Dec 82	A	A,F,AxF	A,AxF	A	A	NM	-
25 Jan 83	-	-	-	-	-	-	A,F,AxF
24 Feb 83	A	-	-	-	A	NM	A,F
9 Mar 83	A,F	-	-	A	A,F,AxF	NM	A
7 Apr 83	A	F	-	A	-	-	A,F,AxF
4 May 83	A	-	-	-	-	NM	A
14 Jun 83	A	A	-	A	-	NM	-
25 Jul 83	-	-	-	-	-	-	A,F,AxF
7 Sep 83	-	-	-	A	-	NM	A
12 Nov 83	A	A	-	A	A	A,F	A
5 Jan 84	A	-	A	A	A	A,AxF	F
1 Mar 84	A	-	-	-	-	NM	-
11 May 84	-	-	NM	-	-	NM	-
3 Aug 84	-	-	NM	-	NM	NM	-
24 Sep 84	A	-	NM	-	NM	NM	-
8 Jan 85	A,F	-	NM	A,F	NM	NM	A

The factors tested for incorporation as model terms were leaf age (A), leaf form (F), their interaction with each other (AxF), and their interaction with tree health (AxH & FxH). A dash indicates that none of these was significant ($p>0.10$). NM indicates that no measurements were made for that date. Leaf age (A) significantly contributed to variation in essential oil content of leaves on the 2 occasions on which it was measured.

Table 3. Mean values of foliage properties of dieback-affected and healthy trees.

Sampling date	Water content				Nitrogen content				Specific weight				Shape				Insect damage [1]			
	unadj.		adj.		unadj.		adj.		unadj.		adj.		unadj.		adj.		unadj.		adj. [2]	
	H	D	H	D	H	D	H	D	H	D	H	D	H	D	H	D	H	D	H	D [3]
13 Sep 82	48.2	50.2	43.2	44.0	1.45	1.56	1.48	1.68	23.7	21.2	29.0	26.4			NM		18.1	21.3	23.7	28.8
3 Oct 82	46.9	48.3	43.6	43.2	1.45	1.58	1.57	1.89	24.1	21.1	26.7	24.6	0.43	0.66	0.42	0.52	13.5	19.4	18.3	26.1
2 Nov 82	49.7	54.0	46.4	46.5	1.53	1.85	1.45	1.55	22.6	17.7	25.4	23.3			NM		10.2	11.3	18.7	21.6
2 Dec 82	56.4	59.8	48.7	49.7	1.71	2.02	1.40	1.70	17.5	14.4	22.8	22.3			NM		8.4	9.1	14.8	17.0
27 Dec 82	56.0	57.4	48.3	47.9	1.47	1.76	1.41	1.25	19.0	16.4	22.5	21.2			NM		11.3	13.5	-	-
25 Jan 83	53.8	58.0	-	-	1.44	1.65	-	-	21.0	16.2	-	-	0.48	0.58	-	-	9.0	14.5	9.7	21.2
24 Feb 83	50.0	51.4	47.4	47.7	1.43	1.60	-	-	22.1	18.2	-	-			NM		9.0	12.0	12.7	22.2
9 Mar 83	50.1	52.6	46.4	53.0	1.47	1.64	-	-	21.7	17.9	23.0	19.2			NM		13.6	17.1	16.7	20.6
7 Apr 83	51.0	54.0	48.2	48.9	1.59	1.73	1.61	1.82	22.7	18.6	21.7	18.5	0.50	0.61	-	-	18.7	25.1	27.3	34.1
4 May 83	51.0	52.2	47.9	48.7	1.63	1.85	-	-	22.2	19.1	-	-			NM		11.7	12.5	16.7	17.9
14 Jun 83	52.8	53.1	51.0	50.5	1.73	1.90	1.70	1.85	21.3	19.5	21.7	19.8			NM		8.8	13.9	-	-
25 Jul 83	48.9	50.5	-	-	1.78	1.92	-	-	23.4	20.2	-	-	0.48	0.67	-	-	10.2	15.1	10.9	25.8
7 Sep 83	51.8	53.8	-	-	1.76	1.86	-	-	22.5	18.9	23.8	20.8			NM		7.2	12.8	9.9	15.3
12 Nov 83	60.2	62.8	47.7	48.4	2.18	2.44	1.16	1.24	16.6	12.6	24.3	22.0	0.34	0.69	0.46	0.73	7.2	8.6	13.4	17.0
5 Jan 84	61.2	64.0	40.9	51.6	1.75	1.89	-	-	15.0	11.7	20.7	17.2	0.31	0.56	0.25	0.58	5.5	9.1	4.9	2.9
1 Mar 84	57.5	55.1	56.7	53.5	1.59	1.59	-	-	17.5	16.5	-	-			NM		3.6	19.1	-	-
11 May 84	53.7	54.7	-	-	1.60	1.62	-	-	19.3	16.7	-	-			NM		5.2	18.4	-	-
3 Aug 84	52.3	52.6	-	-	1.43	1.55	-	-	20.5	17.9	-	-			NM		10.9	20.6	-	-
24 Sep 84	49.9	50.9	43.2	44.6	1.20	1.19	-	-	21.2	18.6	-	-			NM		6.1	16.9	-	-
8 Jan 85	53.5	55.6	48.7	47.9	1.02	1.23	-	-	19.8	16.7	21.5	19.8			NM		9.5	14.1	11.3	21.6

1. Sugar contents were significantly different only on 5 Jan 84. Then the unadjusted means were 5.5%(H) & 4.0%(D), and the adjusted means were 6.1%(H) & 4.6%(D). Tannin contents differed significantly only on 13 Sep 82. Then the unadjusted means were 15.2%(H) & 16.3%(D), and the adjusted means were 14.9%(H) & 18.5%(D).

2. Unadjusted and adjusted mean values (Tables 1 & 2). Dashes indicate they were equivalent. NM indicates that no measurements were made for that date.

3. H = healthy trees, D = dieback trees.

Table 4. Variation in dietary quality variables with age of foliage, averaged over all samples measured.

DQ[1]	Leaf age[2]	Tree health:[3] H	D	t value[4]
water content	Y	61.9±5.6(43)	63.3±5.3(54)	1.259^{ns}
	NM	58.0±5.3(25)	59.4±5.8(44)	0.965^{ns}
	M	53.1±3.8(133)	53.2±4.6(160)	0.258^{ns}
	O	48.1±4.7(117)	49.5±3.7(93)	2.325**
specific leaf weight	Y	15.1±3.2(45)	12.5±3.7(53)	3.694***
	NM	17.4±3.8(25)	14.5±3.3(44)	3.412***
	M	20.5±3.0(133)	18.3±3.5(161)	5.633***
	O	23.5±3.2(117)	20.6±3.2(93)	6.339***
shape	Y	0.38±.13(15)	0.57±.12(20)	4.521***
	NM	0.40±.13(10)	0.60±.13(11)	3.414***
	M	0.51±.12(44)	0.68±.13(52)	6.354***
	O	0.46±.09(36)	0.65±.12(23)	6.867***
nitrogen	Y	1.75±.48(40)	2.04±.56(51)	2.619***
	NM	1.56±.30(22)	1.78±.40(38)	2.238***
	M	1.59±.26(129)	1.73±.24(155)	4.624***
	O	1.48±.24(112)	1.50±.22(87)	0.593^{ns}
soluble sugars	Y	5.4 ±1.8(36)	4.7 ±2.1(47)	1.625*
	NM	6.2 ±2.3(22)	6.3 ±2.5(34)	0.135^{ns}
	M	5.7 ±1.9(114)	5.4 ±1.9(153)	1.082^{ns}
	O	5.7 ±1.8(94)	5.9 ±1.7(64)	0.814^{ns}
tannins	Y	24.0±5.3(32)	23.7±5.5(43)	0.308^{ns}
	NM	18.4±4.7(23)	16.6±3.7(35)	1.641**
	M	16.0±4.0(124)	14.5±3.3(156)	3.341***
	O	15.4±4.3(96)	15.2±3.2(68)	0.342^{ns}
total essential oils	Y	1.3 ±0.3(4)	1.2 ±0.9(5)	0.061^{ns}
	NM	2.2 ±0.9(5)	2.6 ±1.3(5)	0.515^{ns}
	M	2.9 ±2.7(11)	1.7 ±1.0(13)	1.529*
	O	1.8 ±0.3(3)	1.4 ±0.6(4)	1.107^{ns}
insect damage	Y	8.6± 9.5(45)	8.3± 8.4(54)	0.150^{ns}
	NM	8.8± 6.8(25)	11.7± 8.4(43)	1.486*
	M	9.9± 6.7(128)	16.9±10.3(147)	6.566***
	O	12.8± 6.8(113)	20.8±11.2(86)	6.205***

1 dietary quality variable
2 Y = young, NM = nearly mature, M = mature, O = old
3 H = healthy, D = dieback. Values expressed as mean ± standard deviation (numbers of samples)
4 for comparison of mean values for healthy and dieback trees; *** P<0.01, ** P<0.05, * P<0.10, ns P>0.10

Table 5. Dietary quality and herbivory of foliage of trees at site 1 at the peak of the drought and a year later.

Sampling date	Foliage variable	Mean values:[1] Water status[2] NS	S	F(1,6)	Tree health[3] H	DB	F(1,6)
9 Mar 1983	water content	52.0	49.4	4.673^{*}	50.6	51.6	0.333^{ns}
	specified weight	18.4	20.2	5.198^{*}	20.9	17.3	21.039^{***}
	nitrogen	1.67	1.44	33.541^{***}	1.48	1.67	24.192^{***}
	soluble sugars	4.0	4.5	0.869^{ns}	4.4	4.0	0.699^{ns}
	tannins	14.4	21.3	5.721^{*}	17.4	16.9	0.030^{ns}
	% area removed	21.6	17.2	0.856^{ns}	16.6	23.0	1.938^{ns}
1 Mar 1984	water content	52.9	52.6	0.099^{ns}	52.3	53.3	1.827^{ns}
	specific weight	20.3	19.9	0.096^{ns}	21.0	19.2	2.692^{ns}
	nitrogen	1.79	1.92	0.977^{ns}	1.72	1.96	3.630^{ns}
	soluble sugars	6.0	6.3	0.281^{ns}	6.2	6.0	0.109^{ns}
	tannins	13.4	15.2	1.067^{ns}	14.9	13.3	0.899^{ns}
	% area removed	14.3	6.1	5.499^{*}	7.6	14.5	4.025^{*}

[1] Interactions between water status and tree health were never significant (P>0.10) and are not listed. (*** P<0.01; ** P<0.05; * P<0.10; ns P>0.10)

[2] NS = no symptoms of drought stress, S = drought stressed

[3] H = healthy, DB = dieback

Table 6. Regressions of seasonal means of the dietary quality variables against herbivory accumulated during the season, from September 1982 to September 1983.

Quality variable	Regressions fitted: [1] **A** h&d: $r_i = a + b\,q_i + e_i$	VA^2	**B** h: $r_i = a_h + b\,q_i + e_i$ d: $r_i = a_d + b\,q_i + e_1$	$F(1,16)^3$	VA^2	**C** h: $r_i = a_h + b_H\,q_i + e_i$ d: $r_i = a_d + b_d\,q_i + e_i$	$F(1,15)^3$	VA^2
water content		11%	h: r = -2.8 + 0.2 q d: r = +4.1 + 0.2 q	4.39*	25%		<1 ns	20%
specific leaf weight		40%		1.11 ns	40%	h: r = 13.0 - 0.3 q d: r = 74.6 - 3.4 q	7.25**	57%
shape (x100)		47%		<1 ns	-	h: r = +6.0 + 0.02 q d: r = -16.3 + 0.4 q	3.51*	53%
nitrogen content		11%	h: r = 3.1 + 2.3 q d: r = 10.0 + 2.3 q	4.18*	25%		<1 ns	23%
soluble sugar content		16%		14.85***	54%	h: r = 10.5 - 0.7 q d: r = 63.8 - 8.7q	7.76**	68%
tannin content		-		<1 ns	-	h: r = +6.0 + 0.02 q d: r = -16.3 + 0.4 q	3.51*	53%

[1] h = healthy trees, d = dieback trees, r = % foliage area removed, q = dietary quality variable, a & b are constants. Equation(s) are only shown for the highest order model that was a significant improvement over a lower order one.

[2] % variance accounted for = (difference between residual and total mean squares) / (total mean square)

[3] F ratio for testing model improvement = (change in mean square) / residual mean square of the fuller model.
*** P<0.01, ** P<0.05, * P<0.10, ns P>0.10

Table 7. Regressions of seasonal means of the dietary quality variables against herbivory accumulated during the season, from September 1983 to September 1984.

Quality variable	Regressions fitted: **A** h&d: $r_i = a + b\,q_i + e_i$ VA	**B** h: $r_i = a_h + b\,q_i + e_i$ d: $r_i = a_d + b\,q_i + e_i$	F(1,7)	VA	**C** h: $r_i = a_h + b_h\,q_i + e_i$ d: $r_i = a_d + b_d\,q_i + e_i$	F(1,6)	VA
water content	-	h: r = 97.8 - 1.6 q d: r = 108.3 - 1.6 q	52.65^{***}	85%		2.83^{ns}	88%
specific leaf weight	40%	h: r = 10.7 - 0.4 q d: r = 19.4 - 0.4 q	10.06^{**}	72%		$<1^{ns}$	70%
shape (x100)	61%	h: r = 2.8 + 0.02 q d: r = 11.8 + 0.02 q	3.69^{*}	71%		$<1^{ns}$	67%
nitrogen content	15%	h: r = -26.8 + 17.8 q d: r = -18.1 + 17.8 q	29.02^{***}	84%		2.64^{ns}	85%
soluble sugar content	52%	h: r = 10.5 - 1.4 q d: r = 18.5 - 1.4 q	7.06^{**}	73%		$<1^{ns}$	72%
tannin content	0%		22.10^{***}	73%	h: r = 2.0 + 0.1 q d: r = 73.8 - 3.3 q	4.17^{*}	81%

(see Table 6 for explanation of headings)

Table 8. Correlation matrix for seasonal means of dietary quality variables and herbivory accumulated during the season, for the dieback trees during 1982-3.

	rem	wc	spwt	nit	sug	tan	shape
rem	1.000						
wc	.056	1.000					
spwt	-.738**	-.280	1.000				
nit	.203	.718***	-.521	1.000			
sug	-.843***	-.445	.673**	-.291	1.000		
tan	.348	-.431	-.076	-.598*	-.207	1.000	
shape	.705**	-.566	-.334	-.400	-.328	.735**	1.000

df = 7; *** P<0.01, ** P<0.05, * P<0.10
rem = % foliage area removed; wc = water content; spwt = specific leaf weight; nit = nitrogen content; sug = soluble sugar content; tan = tannin content.

Table 9. Correlation matrix for seasonal means of dietary quality variables and herbivory accumulated during the season, for the dieback trees during 1983-4.

rem	1.000						
wc	-.816*	1.000					
spwt	-.030	.007	1.000				
nit	.776	-.970***	.206	1.000			
sug	-.428	.537	.846*	-.342	1.000		
tan	-.696	.853*	-.231	-.931**	.254	1.000	
shape	.174	-.548	.432	.695	.054	-.822*	1.000
	rem	wc	spwt	nit	sug	tan	shape

df = 3 ; abbreviations as in Table 8

Table 10. Partial correlation coefficients, calculated from the data for the dieback trees

$r_{x.y(z)}$ [1]	1982-3 (df=6)		1983-4 (df=2)	
$r_{sug.rem(spwt)}$	-0.693^{*}	$[-0.843^{***}]$	-0.756^{ns}	$[-0.428^{ns}]$
$r_{spwt.rem(sug)}$	-0.428^{ns}	$[-0.738^{***}]$	$+0.690^{ns}$	$[-0.030^{ns}]$
$r_{shape.rem(tan)}$	$+0.707^{**}$	$[+0.705^{**}]$	-0.974^{**}	$[+0.174^{ns}]$
$r_{wc.rem(nit)}$	-0.132^{ns}	$[+0.056^{ns}]$	-0.410^{ns}	$[-0.816^{*}]$
$r_{wc.rem(tan)}$	$+0.243^{ns}$	$[+0.056^{ns}]$	-0.593^{ns}	$[-0.816^{*}]$
$r_{nit.rem(tan)}$	$+0.548^{ns}$	$[+0.203^{ns}]$	$+0.490^{ns}$	$[+0.776^{ns}]$

[1] $r_{x.y(z)}$ is the correlation between x and y, independent of z. Other abbreviations follow Table 8. The ordinary correlation coefficient for x and y from Tables 8 & 9 is shown in square brackets, for comparison.

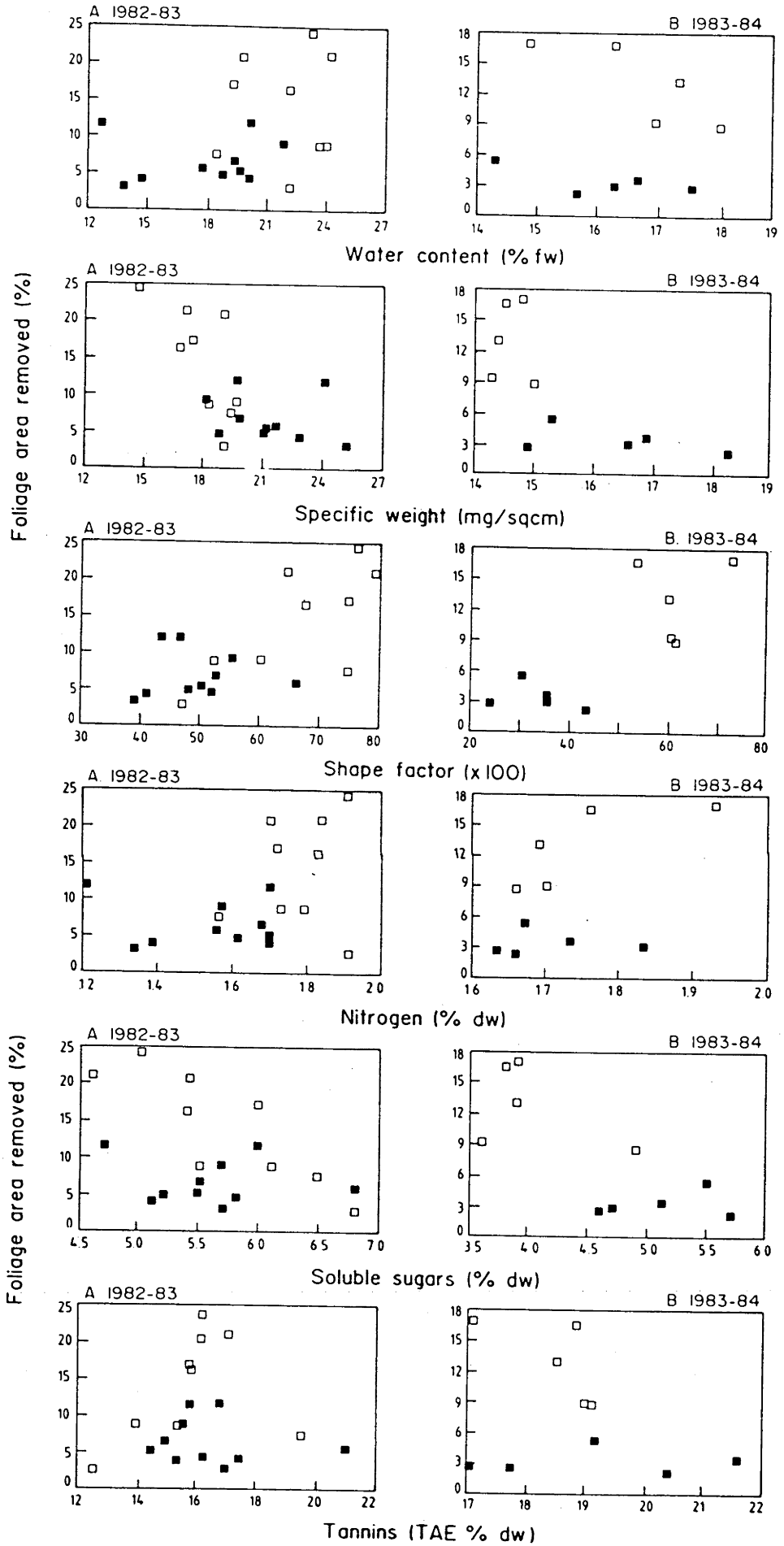
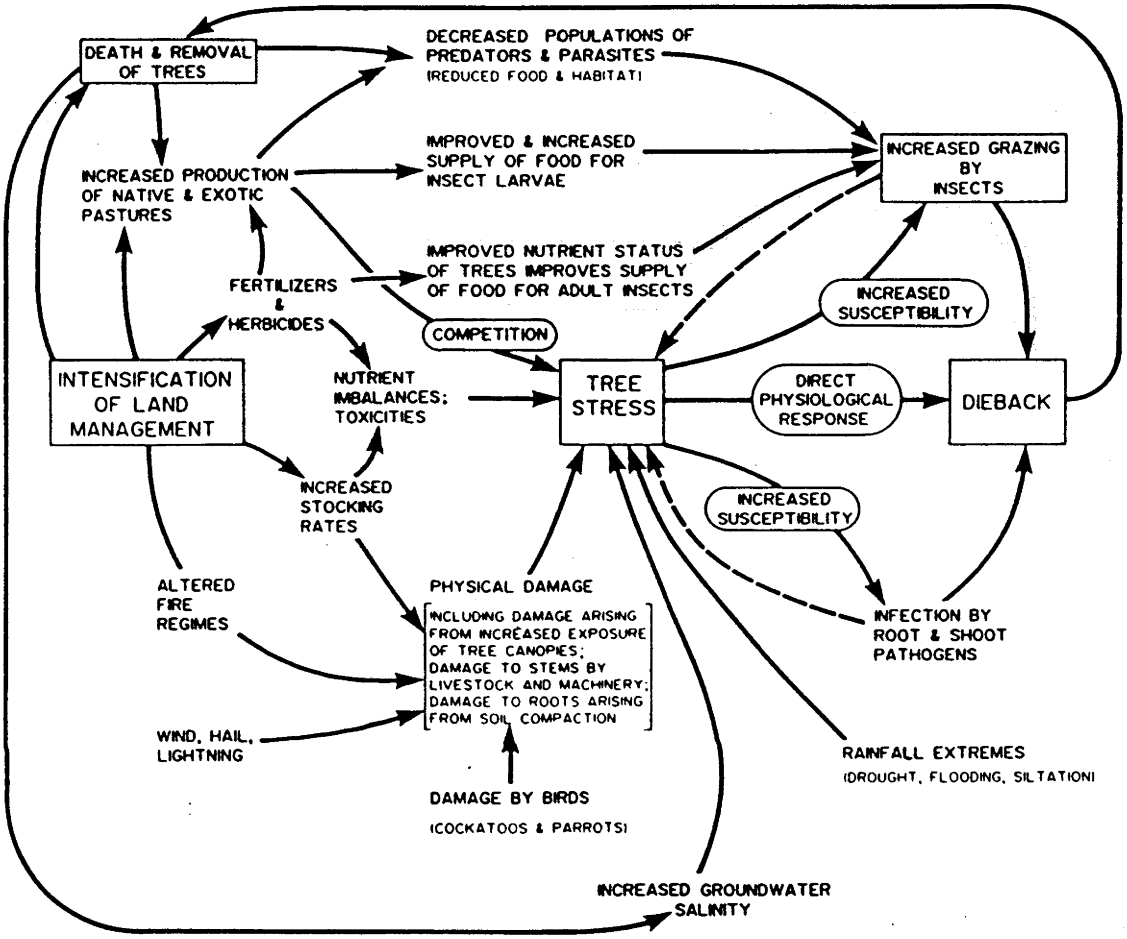
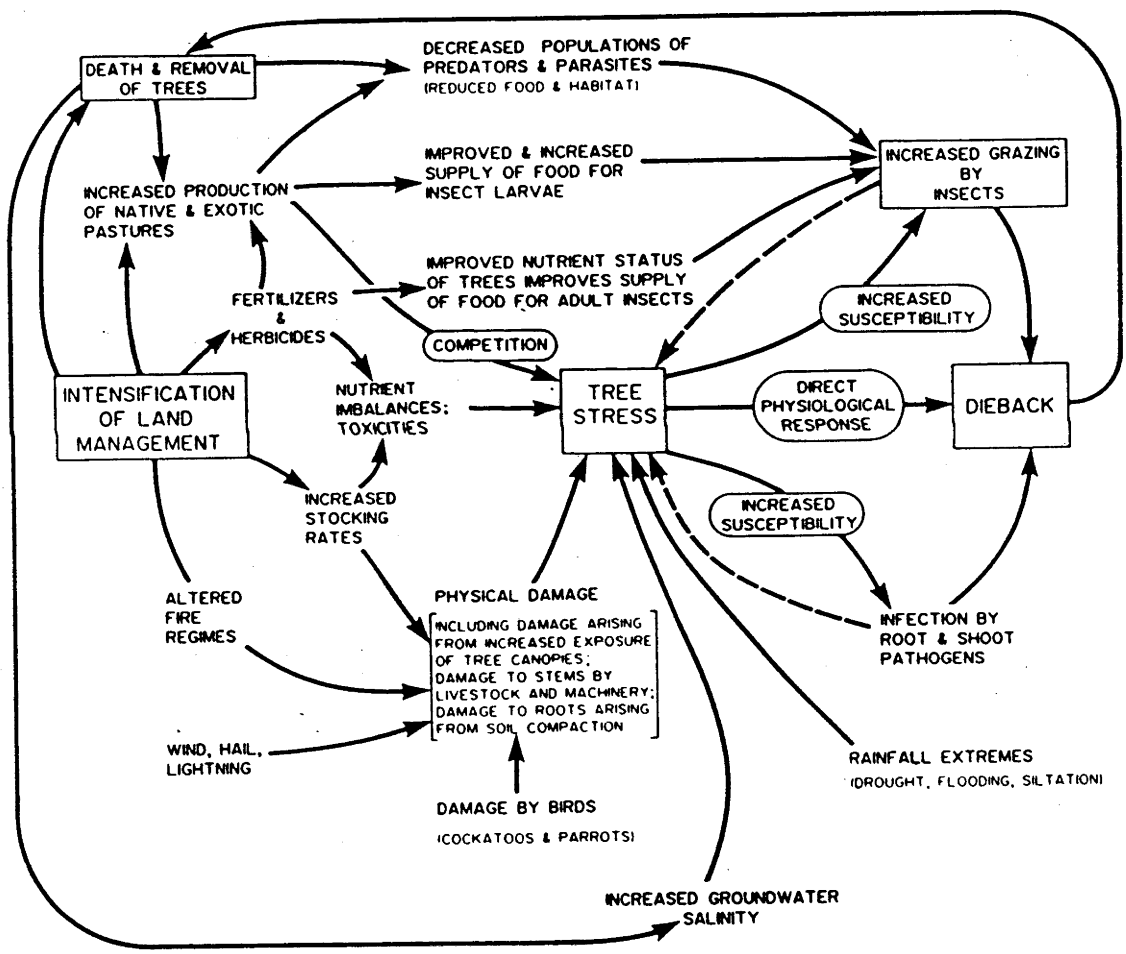


Fig.1. Cumulative herbivory and mean dietary quality of foliage of trees during the 1982-3 growing season (A) and during the 1983-4 growing season (B). Solid symbols represent healthy trees and open symbols represent dieback trees.



The dietary quality of the foliage of E. blakelyi trees with dieback is generally more favourable for insect herbivores than that of healthy trees growing nearby. The foliar dietary properties most likely to indicate that foliage is susceptible to insect grazing are high concentrations of foliar nitrogen and low specific leaf weights.

Does environmental stress enhance the dietary quality of the foliage of dieback and healthy trees, thereby increasing their susceptibility to insect grazing?



DROUGHT AND DIEBACK OF RURAL EUCALYPTS

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ABSTRACT

The possibility that drought causes dieback of eucalypts in rural Australia was investigated. Water potential and canopy condition in dieback and healthy rural Eucalyptus blakelyi and E. melliodora trees were compared during and after an extreme drought in the ACT. All the trees were drought affected, but the extent was independent of the condition of their canopies at the beginning of the study.

INTRODUCTION

Drought has several times been implicated in dieback and death of native trees in Australian forests and woodlands. When the deficiency of rainfall was protracted and severe, dieback proceeded through a sequence of wilting, chlorosis and loss of foliage, and resulted in death of some individuals (Ashton et al. 1975; Pook 1981). Drought may also have acted to predispose trees to fungal infection and insect defoliation in dieback diseases of complex etiology in Tasmania (Palzer 1981; Podger et al. 1980).

These observations have led to speculation that drought may also be a major factor in the widespread decline and death of native trees in rural Australia (Landsberg & Wylie 1983; Pook & Forrester 1984). This is difficult to investigate directly, since current dieback of rural trees may relate to previous drought events and the spatial and temporal occurance of rural dieback is poorly documented. In many regions 'healthy' and 'dieback' trees coexist. If the main reason for their present differences in canopy condition is that they have been affected to different extents by previous droughts, then I hypothesised that the water status of 'dieback' trees should be less favourable than that of their healthy neighbours during an extreme drought.

I tested this hypothesis by comparing predawn water potentials in rural Eucalyptus blakelyi and E. melliodora trees, some with marked canopy dieback and others with healthier canopies, during the course of a year which included several months of extreme drought.

SITES AND METHODS

Trees at two sites at Hall, in the ACT, were monitored from September 1982 to September 1983. The region's mean annual rainfall of 635 mm is spread evenly through the year, but pan evaporation has a marked summer maximum (1626 mm, compared with 50 mm in winter). The first five months of the study were ones of 'extreme drought', according to the widely used Palmer Drought Index (McDonald 1984).

This period was the culmination of the worst drought the Southern Tablelands has experienced in the 71 years for which records are available (Table 1). The drought broke in late March 1983, and the months following varied from 'near normal' to 'very wet' on the Palmer Index.

Both sites are managed for grazing of sheep and cattle. Site 1 is a semi-cleared woodlot on a gentle hillslope with some rock outcrop; the pasture is dominated by Phalaris sp. Site 2 consists of scattered shade trees amongst mixed, unimproved pasture in a valley bottom. Dominant soils in the area are red and yellow podzolics with associated red earths, overlying acid igneous rocks. Salt values are low and pH's are slightly acid to neutral (Walker 1978).

The dominant tree species at the sites are Eucalyptus blakelyi Maiden, and E. melliodora A. Cunn. ex Schau. This alliance occurrs extensively on the grazing lands of the slopes and tablelands of NSW (Milton Moore 1975), and is very susceptible to rural dieback (Duggin 1981). Trees at the study sites exhibited a wide range of canopy conditions. At the beginning of the study trees were classified as 'healthy' or 'dieback' from an assessment of crown size, density, epicormic growth and dead branches (Landsberg & Wylie 1983, modified from Grimes 1978). Thickened growth rings on some of the epicormic stems on the 'dieback' trees indicated a history of dieback extending over at least the last four growing seasons. Five E. blakelyi trees in each category were selected at each site. At the peak of the drought measurements were also made in three E.melliodora trees at each site. All E.melliodora individuals at the sites are 'healthy'. Crown assessments were repeated in February and March 1983, when some trees were visibly drought affected, and again in February and March 1984, a year after the drought had broken.

Since equilibration of water between plant and soil takes place during the night, predawn xylem water potential (predawn ψ) reflects the influence of soil water deficit on plant water status. ψ in cut, leafy shoots was measured in a pressure chamber, with mean values for each tree calculated from measurements in three shoots (Ritchie & Hinkley 1975). All shoots were cut with pole-pruners before dawn and

immediately stored in black plastic bags in a cooled insulated chest. Pressures were read after dawn, but less than 2 hours after cutting. Preliminary tests had indicated that samples handled in this way maintained their predawn potentials for 3 to 4 hours after cutting.

RESULTS

By the end of the drought all the trees had dropped some leaves and had failed to produce any new growth, so that foliage density of all trees was reduced. The foliage of the E. blakelyi trees in which lowest ψ values were measured was dull, and some leaf chlorosis was becoming apparent. There were four trees in this category, two 'healthy' and two 'dieback', all at site 1. During the spring and summer following the drought all the trees initiated a flush of new shoot growth, and by February 1984 all the trees had largely replaced their canopies with an abundance of leaves initiated post-drought (Table 2). None of the trees was sufficiently altered by the drought, or by the subsequent recovery, to cause a change in its initial rating as 'dieback'or 'healthy'.

The variance of ψ amongst trees was analysed for each of the 17 sampling occasions, by two-way ANOVA with site and health ('healthy' or 'dieback') as factors. Similiar analyses were performed on the means, ranges and (log) variances of W, calculated from the pooled data for all 17 occasions. In none of these analyses was tree health a significant source of variation, though site differences were often significant ($P<0.05$). Not suprisingly predawn ψ was often lower in trees at site 2, the better drained site (Fig. 1).

Lowest predawn ψ values were recorded in March 1983, when values ranged from a highest value of -0.74 MPa (a 'dieback' tree at site 2) to a lowest value of -2.54 MPa (a 'dieback' tree at site 1). Mean values at site 1 were -1.78 MPa in E. blakelyi trees and -2.17 MPa in E. melliodora trees. Mean values at site 2 were -1.09 MPa in E. blakelyi trees and -1.44MPa in E. melliodora trees. These values are

within the range of values calculated by Pook (1981) for trees during the 1965 drought. Journet (1979) suggested that E. blakelyi trees under normal conditions regulate water loss in such a way that values below about -18 bars (-1.8MPa) are avoided. Predawn ψ values below -1.8MPa were measured in only four E. blakelyi trees. These were the same two 'dieback' and two 'healthy' trees at site 1 which were most visibly drought affected. Three E. melliodora trees at site 1 also had predawn W values below -1.8 MPa but appeared less affected than the E. blakelyi trees (Table 2).

CONCLUSIONS

The study was undertaken during and after the region's most severe drought on record. It was sufficiently severe to visibly affect all the trees, although there was considerable variation in degree. The least affected individuals suffered only minor canopy thinning resulting from loss of old leaves and a paucity of new growth during the drought. In the most affected individuals this canopy thinning was more pronounced, and some leaf chlorosis was apparent. This variation was also reflected in predawn ψ values of individual trees, which ranged from -0.74 MPa to -2.54 MPa at the peak of the drought.

Yet there was no association between this variation in degree of drought stress experienced by individuals and their initial rating as 'dieback' or 'healthy'. Both the least affected and the most affected trees, in terms of their predawn ψ values at the peak of the drought, were rated as 'dieback'. The four most affected E. blakelyi trees, both in terms of ψ values and canopy appearance, were two 'healthy' and two 'dieback' individuals. Nor was there any evidence 12 months after the drought ended that any 'healthy' trees had acquired lasting symptoms of dieback or that any 'dieback' trees had regained a healthy canopy appearance.

My initial hypothesis was that if rural dieback is mainly the result of previous droughts, then during a severe drought trees with rural dieback should be more affected than their healthier neighbours. The results do not show this.

There could be several reasons for this. Perhaps a different measure of drought response may have yielded different results. Landsberg and Wylie (1983) found that 'dieback' and 'healthy' rural trees differed in their diurnal pattern of water deficit development. This wasn't monitered in the present study. However, predawn ψ is usually agreed to reliabily indicate the influence of soil water deficits on plant water status, and the predawn ψ values I measured agreed well with canopy appearance.

Perhaps the initial hypothesis was at fault. Dieback caused by previous droughts at the sites may have resulted in altered root/shoot ratios which buffered some trees from the influence of the most recent drought. But if less severe previous droughts caused long term dieback in some trees at the sites then it is surprising that the recent, very severe drought did not have a more lasting effect on the canopy appearance of the most drought stressed individuals in this sample. Instead, only a year after the drought, stressed trees initially rated as 'healthy' had recovered dense canopies with very few dead branches or epicormic foliage, and trees rated as 'dieback' had retained a characteristic abundance of dead branches and epicormic foliage despite similiar increases in foliage density (see Table 2).

There is good evidence to show that drought can cause dieback in some circumstances. But my results show that drought is unlikely to have caused the marked dieback of trees at my study sites, and must also cast doubt on the likelihood of drought being a major cause of the non-specific dieback of rural eucalypts in other parts of south eastern Australia.

Table 1. Average Palmer Drought Index for all droughts since 1913 in the Southern Tablelands region, N.S.W. and A.C.T.

Period of Drought	No. of Months	Average Palmer Drought Index[1]
Oct 1913-Mar 1916	30	-2.9
Jun 1918-Nov 1919	18	-2.8
Dec 1925-Sep 1927	22	-1.9
Oct 1936-Feb 1939	29	-1.7
Feb 1944-Oct 1947	45	-2.5
Apr 1954-Aug 1955	17	-2.3
Jan 1957-Sep 1958	21	-2.4
Jan 1965-Aug 1966	21	-2.9
Mar 1967-Aug 1968	19	-3.6
Jan 1965-Aug 1968[2]	40	-3.3
Jun 1972-Sep 1973	16	-2.9
Feb 1979-Dec 1982[3]	47	-4.3

[1] Calculations of averages (McDonald pers. comm.) based on McDonald (1984). Index values of 0.49 to -0.49 indicate 'near normal' conditions, values of -0.50 to -0.99 indicate 'incipient drought', values of -1.00 to -1.99 indicate 'mild drought', values of -2.00 to -2.99 indicate 'moderate drought', values of -3.00 to -3.99 indicate 'severe drought', and values velow -4.00 indicate 'extreme drought'.

[2] Alternative calculation based on the assumption that rain from Sep 1966 to Feb 1967 was insufficient to break the drought.

[3] the drought continued until Mar 1983.

Table 2. Visual assessments of tree vitality for the 7 trees which experienced water potentials below -18 bars during the drought.

Species[1]	ψ [2]	Health[3]	Visual assessment of tree vitality[4] Feb-Mar 1983	Feb-Mar 1984
blak	-1.92	H	4.0+4.0+2.5+2.0=12.5	4.0+6.0+4.0+2.5=16.5
blak	-2.09	DB	2.0+3.0+1.0+1.5= 7.5	2.0+4.0+1.0+1.5= 8.5
blak	-2.12	H	4.0+5.0+3.0+2.0=14.0	4.0+5.0+4.0+2.5=15.5
mell	-2.12	H	4.0+5.0+2.5+2.0=13.5	4.0+6.0+3.0+2.5=15.5
mell	-2.12	H	2.0+6.0+3.0+2.5=13.5	2.0+7.0+4.0+2.5=15.5
mell	-2.27	H	3.0+6.0+4.0+2.5=15.5	3.0+7.0+4.0+2.5=16.5
blak	-2.54	DB	1.5+1.5+1.0+1.5= 5.5	1.5+3.0+1.0+1.5= 7.0

[1] blak is E. blakelyi and mell is E. melliodora

[2] Lowest predawn ψ measured (MPa)

[3] H is 'healthy' and DB is 'dieback'

[4] Ratings are expressed as the sums of scores for : crown size + crown density + lack of dead branches + lack of epicormics = total score. Note the increase in crown density scores for all trees between 1983 and 1984.

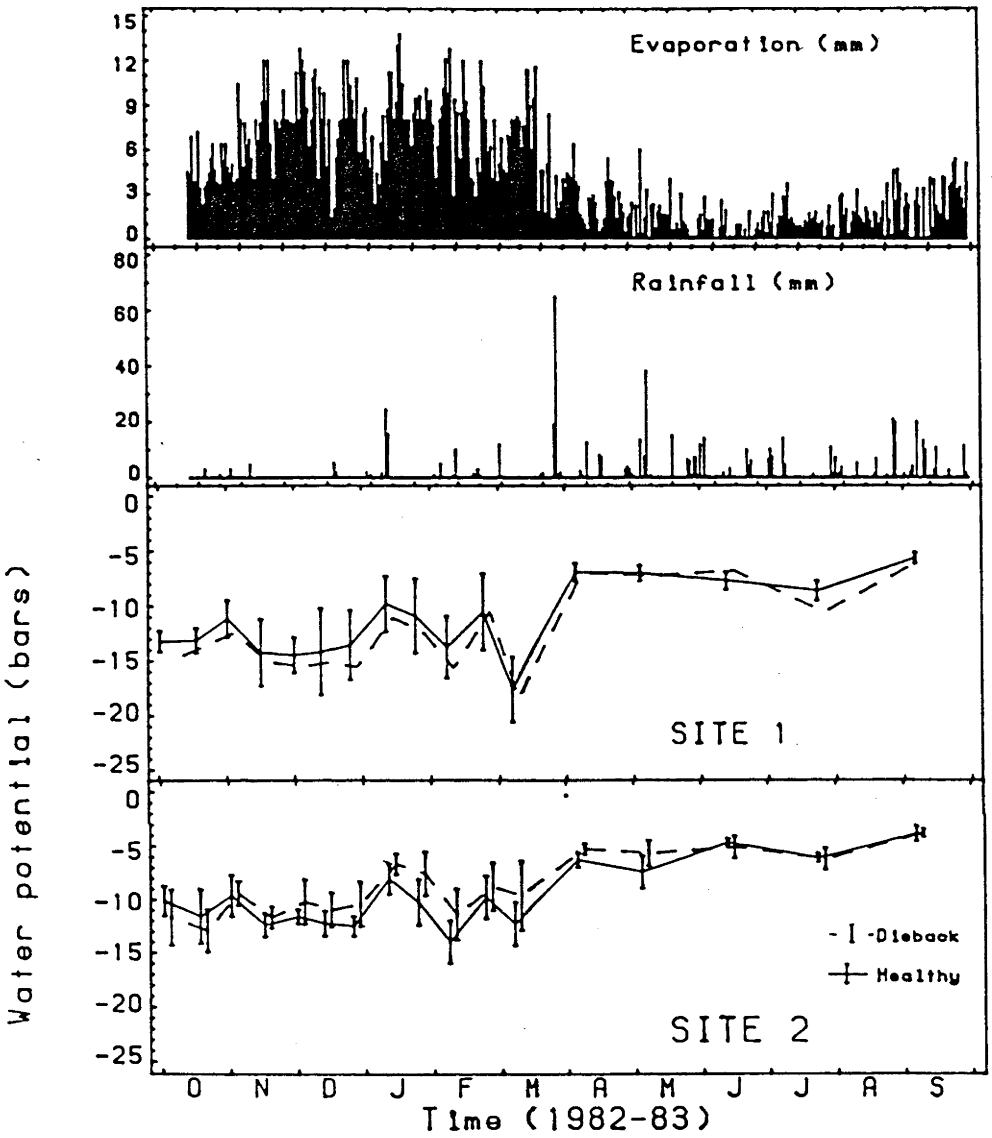

Fig.1. Predawn ψ in groups of study trees during the course of the year. Solid lines join mean base ψ values for 'healthy' E. blakelyi trees, dashed lines join mean base ψ values for 'dieback' E. blakelyi trees, and triangles show mean values for E. melliodora trees, which were all healthy. Error bars show 95% confidence intervals. Daily rainfall and (pan) evaporation data are from the CSIRO Ginninderra Experiment Station, 4km away.

THE EFFECT OF STRESS ON THE NUTRITIONAL QUALITY OF THE FOLIAGE OF SEEDLINGS OF DIEBACK-AFFECTED AND HEALTHY EUCALYPTS

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ABSTRACT

Canopy dieback of Eucalyptus blakelyi trees is often associated with defoliation by insects: the foliage of trees with dieback is nutritionally superior for insects and is more heavily damaged by them. I investigated whether differences in the nutritional quality of foliage were genetically determined, or caused by environmental stress. In a series of glasshouse experiments, with seedlings and grafted plants derived from dieback and healthy populations of trees, I tested the influence of: depletion of nutrients, addition of excess phosphate, drought, waterlogging, and saline waterlogging on the nutritional quality of foliage. Differences in the foliar properties of plants from different genetic sources were not consistent with the differences between the source populations. Most of the environmental stresses applied caused a reduction in foliar quality, (decreased water and nitrogen contents, and increased specific leaf weights). I hypothesize that the enhanced nutritional quality of the foliage of dieback-affected trees is more likely to be a consequence of benign growing conditions (e.g. improved soil fertility), than of environmental stress. Field data for soil properties and the effect of drought on mature trees are consistent with this view.

INTRODUCTION

Dieback of native trees on farms - rural tree dieback - is increasing in severity in many regions of Australia, particularly where farms have long been managed for grazing of sheep and cattle. Although its causes are poorly understood it is often associated with increased damage of tree canopies by insects. Where this occurs trees often differ markedly in their susceptibility to dieback and the associated insect grazing: affected stands of farm trees commonly include healthy individuals as well as those suffering dieback (Kile 1981; Landsberg submitted b; Wylie & Johnston 1984).

This difference in susceptibility could be a consequence of previous defoliations (Landsberg submitted f), of genetic differences, or of differences in the immediate environment of the trees. It has often been suggested, for example, that management of farms for livestock production may impose stresses on farm trees which could increase their susceptibility to grazing by insects. Possible sources of stress which are commonly cited include:
(a) alteration of the hydrological cycle because trees and pasture cause differences in the interception, infiltration or transpiration of rainwater;
(b) altered nutrient balance because of the use of fertilizers (particularly superphosphate) or nutrient transfer by livestock;
(c) nutrient depletion, because of erosion or competition between trees and pasture;
(d) and salinization, because of excessive tree clearance in susceptible catchments
(Anon. 1985; Boyd 1965; Breckwoldt 1986; Johnston & Wylie 1984; Kile 1981; Landsberg & Wylie 1983).

In earlier studies I showed that the dieback of Eucalyptus blakelyi Maiden trees on pastoral properties in the Australian Capital Territory, was associated with defoliation by insects. The foliage of trees with dieback tended to be nutritionally superior for insects, and was more heavily grazed by them (Landsberg submitted c). Foliage from dieback trees contained more water and nitrogen, less soluble sugar, tannin and volatile oil, and had lower specific leaf weights than foliage of similar age from neighbouring healthy trees.

In the study described here I investigated the extent to which the nutritional quality of E. blakelyi foliage was genetically determined, and the extent to which it was altered by the types of stress which trees could encounter on farms. I did this in a series of glasshouse experiments in which seedlings from dieback and healthy trees were deprived of nutrients, supplied with excess phosphate, droughted, waterlogged, and waterlogged with saline solution.

Because the foliage of eucalypt seedlings differs morphologically and physiologically from the adult-form foliage on mature trees (Blake 1980; Jacobs 1955), I repeated one of the experiments using plants grown from cuttings from healthy and dieback trees grafted onto a common, cloned rootstock. The foliage of these grafted plants closely resembled that of the adult-form foliage on the trees from which the cuttings were taken.

METHODS

PLANT MATERIAL

Seed for the experiments was collected from two isolated stands of E. blakelyi trees growing on grazing properties near Hall, in the Australian Capital Territory. All the trees in one of the stands had dieback; the trees in the other stand all appeared healthy. Cuttings of terminal shoots were collected from a third stand of trees (about 5 km from the dieback stand and 2 km from the healthy stand), which consisted of both healthy and dieback trees. I had monitored trees in this stand in earlier studies (Landsberg 1985 & submitted b & c).

Seed was germinated in a shallow layer of peat overlying coarse sand, and seedlings were transferred to 15 cm free-draining plastic pots containing a sand-vermiculite-pearlite mixture when they had 4-8 leaves. Cuttings were chosen which contained swollen leaf buds in their leaf axils. Most of each of their leaves were trimmed off under water at the time of collection, and the trimmed cuttings were

transported to a glasshouse in polythene bags. There they were bottle-grafted onto rootstock which had been cloned from a single E. blakelyi tree from a different provenance, so that any influence of the root stock on foliar properties was similar for all scions. Success rate was low and only 12 of the grafted scions grew vigorously. These plants were much woodier than the seedlings and had adult-form foliage. They were grown in 30 cm plastic pots containing a sand-vermiculite-pearlite mixture.

GROWING CONDITIONS

All plants were grown in a naturally-lit glasshouse with partial temperature control (5°C to 35°C range). Pre-treatment (Table 1), which continued until seedlings were about 30 cm tall, consisted of irrigation daily, or more frequently in hot weather, with balanced nutrient solution (modified from Ingestad 1971 by the addition of extra iron). Treatments (Table 1) were continued until plants were about 60-70 cm tall, or until the foliage of the most stressed plants began to develop necrotic patches. The duration of these treatments varied seasonally (Table 1).

NUTRITIONAL QUALITY OF FOLIAGE

Foliage was sampled by cutting discs of known area from all fully expanded leaves on each plant. Samples were collected from before dawn till one hour after dawn, to minimize differences caused by diurnal variations in leaf properties. They were frozen in liquid nitrogen immediately after collection, then stored in liquid nitrogen until they could be weighed, then lyophilized and reweighed, after which they were ground to a powder. This was stored at -15°C in stoppered vials above a desiccant until it could be analyzed, up to a year later. The nutritional quality variables and their methods of analysis are described more fully elsewhere (Landsberg submitted c). The variables measured were: water content (per fresh weight of leaf); specific leaf weight (dry weight per unit area); content of total soluble sugars, total non-structural carbohydrates and starch (glucose specific assay following enzymatic hydrolysis, Azcon-Bieto &

Osmond 1983); total nitrogen content (Technicon auto-analyzer determination on micro-Kjeldahl digest); and tannin content (relative astringency in a haemoglobin solution against a tannic acid standard, Schultz et al. 1981). Volatile oils were measured for the drought stress experiment only, by gas chromatography.

STATISTICAL ANALYSIS

I analyzed each experiment using ANOVA subroutines from the Genstat computer program (Alvey et al. 1982), to test whether the source of seed or cuttings (healthy or dieback trees), the stress treatments (Table 1), or the interaction between source and treatment, contributed significantly to the variance in each of the nutritional quality variables measured. Total non-structural carbohydrate values, which are the sum of sugar and starch values, were not tabulated because the significance of their F-values always followed the same trend as those of the soluble sugar values.

RESULTS

INFLUENCE OF PLANT SOURCE

Plant source did not contribute significantly to variation in the contents of water, nitrogen, sugar or volatile oils in foliage, in any of the experiments (Tables 2, 3 & 4). There was a tendency for the foliage of plants derived from dieback trees to have higher specific leaf weights than that of plants from healthy trees, and, at least in the excess phosphate experiment, these higher specific leaf weights appeared to reflect higher concentrations of carbon-based compounds such as starch and tannin. Foliage from the grafts and seedlings displayed the same trends although they were derived from different stands of trees. Thus the difference between plants from dieback and healthy trees was unlikely to have arisen by chance. However this difference in specific leaf weights was opposite to that measured in mature trees. E. blakelyi trees with dieback had lower specific leaf

weights than did healthy neighbouring trees, and were more damaged by insects (Landsberg submitted c). I speculated that such a relationship could be causal, if the area of foliage which insects consume is partly dependent on the biomass it represents. Then, all other things being equal, insects will consume a greater area of foliage with low, rather than high, specific leaf weights.

Therefore the only consistent difference in the nutritional quality of the experimental plants' foliage that could be attributed to genetic influences could not account for the differences in the nutritional quality of the foliage of mature trees, and was unlikely to have caused their different susceptibility to grazing by insects.

INFLUENCE OF STRESS TREATMENTS

Most of the experimental treatments caused differences in at least some of the nutritional quality variables measured (Tables 2, 3 & 4). The only exception to this was the excess phosphate experiment. The phosphate concentrations used, 1.6 mM (about 50 ppm) and 3.2 mM (about 100 ppm), represent the middle to upper range of concentrations likely to be found in fertilized pasture soils (Russell 1986), yet they did not significantly affect any of the nutritional parameters measured. Groves and Keraitis (1976) found that similar concentrations of N and P had little effect on the growth of E. pilularis seedlings, even after 16 weeks. While these results do not necessarily mean that phosphate fertilizer applied to mature trees over a much longer time will likewise have little effect on the trees, they do show that, in the short term, eucalypt seedlings are relatively insensitive to moderately high phosphorus concentrations.

The other experimental treatments had a variable effect on the concentrations of tannin and sugar in the seedlings' foliage (Tables 2 & 3). Tannin content was increased by nutrient withdrawal (low nutrient treatment in the nutrient extremes experiment), was decreased by saline waterlogging, and was not changed significantly by the other stresses. Other studies have also shown that the concentration of phenolic acids in foliage (of which tannins are a subset) tends to increase when the supply of nutrients is limited (e.g. Del Moral 1972,

Ohmart et al. 1985, Waring et al. 1985). For sunflowers at least this appears to be a general response to other stresses (Del Moral 1972). This led Del Moral to suggest that phenolic acids originated as regulators of various metabolic systems under stress. My results only partially support this hypothesis, but this may be because tannins constitute a rather diverse subset of plant phenolics. As a group, tannins are characterized by their ability to coagulate proteins, a property likely to be of greater relevance in deterring herbivores than in plant metabolism (Swain 1979). However, at least for eucalypts, the effectiveness of foliar tannins in deterring herbivory also appears to be questionable (Fox & Macauley 1977; Landsberg submitted f).

The soluble sugar content of foliage was also affected differently by different stresses. Limited supply of nutrients caused a decrease in soluble sugar, and drought stress caused an increase (Tables 2 & 3). The foliar nitrogen content of both groups of plants was depressed, and it is therefore likely that photosynthetic rates and the production of photosynthate were also depressed (Mooney et al. 1978). This is the probable explanation of the decreased content of soluble sugars in the foliage of the nutrient-limited plants. However, during water stress translocation of photosynthate is also depressed (Hsiao 1973); an imbalance between the depression in production and translocation of photosynthate could give rise to the increase in the foliar soluble sugar content of the drought-stressed plants. The accumulation of solutes such as soluble sugars may also indicate that osmotic adjustment was occurring in the leaves of the droughted plants (Munns et al. 1979). Some osmotic adjustment may also have occurred in the salt-stressed plants. Though this treatment did not cause significant differences in either soluble sugars or starch, the ratio of sugars (low molecular weight solutes) to starch (high molecular weight) was higher in the salt-stressed plants. (Ratios were 2.17 for saline-waterlogged, and 1.8 for both waterlogged and well-drained treatments; $F=2.873$; $df=2,22$; $P<0.10$)

Volatile oils were measured only in the foliage of plants in the drought experiment (Table 4). Although the foliage of the drought-stressed plants contained significantly more α-pinene and tended to contain more β-pinene than that of well-watered plants, the

concentration of the major volatile oil, cineole, and of total volatile oils, did not differ significantly between the two groups of plants. Since the foliage of mature dieback trees, which were susceptible to insect grazing, tended to contain less volatile oil than the less susceptible healthy trees, the drought stress treatment is not likely to have increased the susceptibility of the seedlings' foliage to insect grazing.

Notwithstanding variable effects on tannins and sugars, there were striking similarities in the effects of most of the stresses applied. The content of water and nitrogen in foliage was decreased, and specific leaf weights were increased, after nutrient depletion, drought, waterlogging and saline waterlogging (Tables 2 & 3). Thus stress generally caused a deterioration in the nutritional quality of seedlings' foliage. In contrast, enhanced nutritional quality of foliage was always associated with 'benign' growing conditions, consisting of a regular supply of balanced nutrients in moderate to high concentrations. This was true of foliage of both seedlings and grafted plants (Tables 2 & 3). The foliage of the grafted plants had higher specific leaf weights and lower water and nitrogen contents than that of comparable seedlings; in this it more closely resembled the foliage of the mature trees from which the cuttings were taken (Landsberg submitted c). However, variation in the foliage of both seedlings and grafts was qualitatively very similar, showing that the nature of the variation was independent of the morphology of the foliage.

DISCUSSION

The effect of stress in these experiments was contrary to much of the prevailing theory on the effect of stress on the nutritional quality of foliage and subsequent herbivory on it. High populations of herbivorous insects are often associated with stressed host trees, and this is thought to relate to reductions in the plants' defensive mechanisms coupled with alterations in their nutrient balance (Mattson & Addy 1975). White (1974, 1976, 1984) has suggested that this may be because stress causes an increase in the abundance in plant tissues of

nitrogen available for young herbivorous insects, thus enhancing their chances of survival.

Although many studies (reviewed in Stewart & Larher 1980) have demonstrated that stress generally induces changes in nitrogen composition which often lead to an increase in the proportion of soluble nitrogen compounds in plant tissues, the effect of stress on the total concentration of nitrogen in plants appears to be more variable. Both the severity and the duration of the stress influence its consequences. For example, when water stress develops gradually, adaptive changes, such as restriction of canopy development and increase in the growth of roots relative to shoots, occur well in advance of physiological responses such as osmotic adjustment and stomatal closure (Bradford & Hsiao 1982). As a result of such adaptive changes, plants faced with moderate environmental stress may be able to largely avoid severe tissue stress, though at the cost of reduced growth. Under these conditions the concentration of nitrogen in plant tissues will depend on the balance between a reduction in its supply (as a result of reduced uptake of soil nitrogen), and a reduction in the demand for nitrogen (associated with the suppression of plant growth): under water stress both accumulation and depletion of total nitrogen in plant tissues have been reported (Bradford & Hsiao 1982). Similarly Munns and Termaat (1986), in their review of whole plant responses to salinity, concluded that the pattern of response of total foliar nitrogen to salinity was quite variable: increases, decreases and no change have all been reported.

A relevant example of this variability in plant response is the contrast between my results and those of Miles *et al*. (1982), who studied a very closely related species of eucalypt. When they applied water stress to *E. camaldulensis* seedlings, the content of total nitrogen in foliage increased, in contrast to my results with *E. blakelyi* seedlings. However Miles *et al*. measured seedling response to a severe stress of relatively short duration; they withheld water from previously well-watered plants until the plants wilted. Thus the changes in foliar nitrogen that they measured would largely reflect responses of leaf physiology to water stress. I grew plants under less severe water stress (plants were watered at the onset of wilting), for a longer duration (about 6 wilting cycles). During this

time growth of the stressed plants was significantly depressed (the mean height of the well-watered plants was 68 cm, compared with 56 cm for the stressed plants; $F=41.64$, $df=1,16$, $P<0.01$). Thus my measurements also reflect adaptive changes and responses at the whole plant level. Corroborative field studies suggest that this longer term response may be very similar to that of mature trees to natural drought.

In earlier studies I had measured the effect of a very severe natural drought on the canopy condition, pre-dawn water potentials, and foliar nutritional quality of mature healthy and dieback E. blakelyi trees growing in the stand of trees from which I collected cuttings for grafting (Landsberg 1985 & submitted c). The effect of this drought on the nutritional quality of the foliage of the most stressed trees was similar to that of experimental drought on seedlings' foliage. In addition, the foliage of the most stressed mature trees was less damaged by insects than that of less stressed trees (Landsberg submitted c).

There is also some evidence that soil under dieback trees at these sites may be more fertile than the soil under nearby healthy trees (Table 5), a difference which the glasshouse experiments suggest could contribute to the enhanced nutritional quality of the foliage of the dieback trees. Russell (1986) has noted that the general improvement in the nutrient status of soils under improved pasture is often associated with a very uneven pattern of concentration of nutrients in topsoils because of their redistribution in animal excreta. In particular, nutrients may become concentrated in preferred 'camps' under some trees.

White (1984) has suggested that more extreme forms of stress, sufficient to cause severe wilting or scorching of plants, may cause foliage deterioration and may thus have an opposite effect to milder forms of stress. If this is generally true, then it may indicate that the stresses I applied were unrealistically extreme. I doubt this, since neither the glasshouse-grown plants I studied, nor the mature E. blakelyi trees which were drought-stressed, developed severe leaf chlorosis or necrosis; no plants died under stress and all recovered quickly when the stresses were relieved. In addition, the stresses I

applied were probably realistic, in that they did not represent the extremes to which trees may become exposed in highly modified grazing pastures. For example, several species of eucalypts were successfully re-established in catchments in Western Australia that were suffering secondary salinization following tree clearance and pasture establishment; chloride concentrations of groundwater in these catchments ranged from 2000-5500 mgl^{-1} (Biddiscombe *et al.* 1985), compared with 2130 mgl^{-1} used in my study.

Despite the strong body of theory linking stress of plants with an increase in their susceptibility to damage by herbivores, there have been surprisingly few detailed studies of the influence of stress on the nutritional quality of tree foliage. My studies have shown that several kinds of stress caused deterioration in the nutritional quality of *E. blakelyi* plants grown under controlled conditions, and that a natural drought had a similar effect on the foliage of mature trees. Thus these studies provide no support for the hypothesis that stresses associated with farm management have increased the susceptibility of farm trees to grazing by insects. A more plausible alternative hypothesis is that the improvement of soil nutrient status generally associated with pasture improvement has also enhanced the nutritional quality of trees growing amongst pasture. If the distribution of nutrients in the topsoil is uneven then enhancement of foliar nutritional quality will be most marked for trees growing in the most fertile localities; I suggest that it is these trees which will be most susceptible to grazing by insects.

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Table 1. Details of the experiments.

Plant material[1]	Irrigation solutions[2]	Experimental treatments[3]
A. Nutrient extremes experiment on seedlings:		
3H & 3DB seedlings per tmt (= 18 plants)	S1 = balanced nutrients (5mM N) S2 = balanced nutrients (2.4mM N) S3 = tapwater (0mM N)	Pre-treatment = irrigation with S2 for 4 weeks (summer). Treatments = irrigation with S1 (high nutrients), S2 (moderate nutrients) or S3 (low nutrients) for 4 weeks (summer).
B. Nutrient extremes experiment on grafted cuttings		
3H & 3DB grafts per tmt (= 12 plants)	S1 = balanced nutrients (5mM N) S2 = tapwater (0mM N)	Pre-treatment = irrigation with S1 for 8 weeks (autumn). Treatments = irrigation with S1 (high nutrients) or S2 (low nutrients) for 12 weeks (winter).
C. Excess phosphate experiment:		
9H & 9DB seedlings in tmt 1, 5H & 5DB seedlings in tmts 2 & 3 (= 38 plants)	S1 = balanced nutrients (3mM N); P is 0.16mM S2 = S1 plus added NaH_2PO_4 so that P is 1.6mM S3 = S1 plus added NaH_2PO_4 so that P is 3.2mM	Pre-treatment = irrigation with S1 for 10 weeks (winter). Treatments = irrigation with S1 (.16mM P), S2 (1.6mM P) or S3 (3.2mM P) for 9 weeks (spring).
D. Drought experiment:		
5H & 5DB seedlings per tmt (= 20 plants)	Balanced nutrients (3mM N)	Pre-treatment = irrigation for 7 weeks (spring). Treatments: surface of pots covered with foil and pots placed on saucers. Well-watered tmt = frequent irrigation Droughted tmt = plants irrigated when they began to wilt (average interval 4.6 days). Treatments were continued for 4 weeks (summer).
E. Waterlogging and salinity experiment:		
5H & 5DB seedlings per tmt (= 30 plants)	S1 = balanced nutrients (3mM N) S2 = S1 plus 40mM NaCl & 10mM $MgCl_2$; the concentration of salts was increased to this level over a period of 10 days	Pre-treatment = irrigation with S1 for 10 weeks (winter). Well-drained tmt = frequent irrigation with S1 Waterlogged tmt = pots placed on large saucers which were kept full by irrigation with S1 Waterlogged & saline tmt = similar to waterlogged tmt, but using S2.

1 Plants grown from seed or cuttings collected from healthy (H) or dieback (DB) trees.

2 The balanced nutrient solutions contained (by weight) 100N (as $60NO_3^-$ & $40NH_4^+$), 65K, 13S, 11P, 8.5Mg, 7Ca, 3Fe, 0.40Mn, 0.20Bo, 0.03Cu, 0.03Zn, 0.007Mo. Stock solution was diluted with tapwater to give the N concentrations shown.

3 Growing condition are described in the text.

Table 2. Nutritional quality of foliage of seedlings and grafts after experimental treatments.

Treatment[1]	Nutritional quality of foliage:[2] % Water			Sp.wt.(mg cm^{-2})			% Nitrogen			% Tannin			% Sugar			% Starch		
	Mn	H	DB	Mn	H	DB	Mn	H	DB	Mn	H	DB	Mn	H	DB	Mn	H	DB
A. Nutrient extremes (seedlings):																		
Mean	72.7	72.0^{a}	72.4^{a}	4.4	4.2^{a}	4.5^{a}	2.63	2.59^{a}	2.66^{a}	15.2	15.0^{a}	15.5^{a}	4.4	4.1^{a}	4.7^{a}			
High nutr.	72.8^{z}	73.6	72.1	4.4^{z}	4.1	4.7	3.40^{y}	3.45	3.36	14.2^{y}	16.6	11.7	5.1^{y}	4.3	5.8			
Mod nutr.	74.7^{y}	74.8	74.6	3.7^{y}	3.4	3.9	3.10^{y}	2.95	3.24	12.3^{y}	13.5	11.2	5.2^{y}	4.4	5.9			
Low nutr.	69.0^{x}	67.8	70.3	5.0^{x}	4.9	5.1	1.38^{x}	1.39	1.37	19.2^{x}	14.8	23.7	3.0^{x}	3.6	2.4			
B. Nutrient extremes (grafted cuttings):																		
Mean	58.6	59.4^{a}	57.9^{a}	13.7	12.8^{a}	14.5^{b}	1.80	1.85^{a}	1.74^{a}	17.9	17.0^{a}	18.9^{a}						
High nutr.	62.5^{y}	64.0	61.0	12.1^{y}	10.7	13.4	2.47^{y}	2.59	2.36	17.3^{x}	15.6	19.0						
Low nutr.	54.7^{x}	54.7	54.7	15.2^{x}	14.9	15.6	1.12^{x}	1.12	1.12	18.6^{x}	18.3	18.8						
C. Excess phosphate:																		
Mean	72.7	73.0^{a}	72.5^{a}	5.4	5.1^{a}	5.7^{b}	3.27	3.31^{a}	3.22^{a}	17.9	16.9^{a}	18.9^{b}	5.6	5.8^{a}	5.3^{a}	3.5	3.1^{a}	4.0^{b}
0.16mM P	72.9^{x}	72.9	73.0	5.4^{x}	5.1	5.7	3.21^{x}	3.25	3.17	18.6^{x}	17.7	19.4	5.5^{x}	5.7	5.2	3.1^{x}	2.9	3.2
1.6mM P	72.4^{x}	73.3	71.5	5.4^{x}	5.1	5.8	3.25^{x}	3.34	3.16	16.5^{x}	15.1	17.8	5.7^{x}	5.9	5.4	4.0^{x}	2.9	5.2
3.2mM P	72.7^{x}	72.8	72.7	5.3^{x}	5.0	5.6	3.40^{x}	3.42	3.38	18.1^{x}	17.2	19.0	5.8^{x}	6.1	5.5	3.8^{x}	3.6	4.0
D. Drought:																		
Mean	70.1	69.4^{a}	70.9^{a}	5.5	5.7^{a}	5.4^{a}	3.46	3.41^{a}	3.50^{a}	19.0	19.3^{a}	18.6^{a}	7.0	7.2^{a}	6.8^{a}	5.8	6.2^{a}	5.5^{a}
Well watered	74.7^{x}	74.3	75.1	4.6^{x}	4.5	4.6	4.20^{x}	4.10	4.30	20.3^{x}	22.3	18.3	5.0^{x}	4.9	5.0	1.9^{x}	2.1	1.8
Droughted	65.5^{y}	64.4	66.6	6.5^{y}	6.8	6.3	2.72^{y}	2.73	2.71	17.7^{x}	16.4	19.0	9.0^{y}	9.4	8.7	9.7^{y}	10.3	9.2
E. Waterlogging and salinity:																		
Mean	70.8	71.0^{a}	70.5^{a}	6.1	5.8^{a}	6.5^{b}	2.97	2.96^{a}	2.97^{a}	18.0	17.4^{a}	18.6^{a}	5.6	5.6^{a}	5.5^{a}	3.7	4.1^{a}	3.4^{a}
Well drained	72.4^{x}	72.7	72.0	5.5^{x}	5.2	5.9	3.21^{x}	3.25	3.17	18.6^{x}	17.7	19.4	5.7^{x}	5.7	5.8	3.3^{x}	3.2	3.5
Waterlogged	70.8^{y}	70.3	71.3	6.3^{y}	6.1	6.6	2.70^{y}	2.51	2.90	19.5^{x}	19.3	19.7	5.0^{x}	5.7	4.3	4.8^{x}	6.9	2.7
Waterlogged & saline	69.1^{z}	69.8	68.3	6.6^{y}	6.1	7.0	2.99^{x}	3.14	2.84	15.9^{y}	15.1	16.6	5.9^{x}	5.5	6.4	3.1^{x}	2.3	3.9

1 Details of treatments are shown in Table 1.

2 Details of measurement techniques are outlined in text. Mn refers to mean values, H refers to seed or cuttings collected from healthy trees, and DB from dieback trees. Means which are not significantly different share the same superscript (from t = difference between means / standard error of the difference, $P<0.10$).

Table 3. F-values for tests of the significance of the contribution of treatments and source of plant material to explaining variance in dietary quality of foliage (ANOVA).

Experiment	Foliage nutritional quality: Water	Sp.wt.	Nitrogen	Tannin	Sugar	Starch
A. Nutr. extremes (seedlings):						
plant source (df = 1,12)	0.087^{ns}	1.438^{ns}	0.064^{ns}	0.145^{ns}	1.702^{ns}	
treatment (df = 2,12)	9.987^{***}	5.395^{**}	25.715^{***}	9.167^{***}	10.106^{***}	
interaction (df = 2,12)	1.220^{ns}	0.180^{ns}	0.216^{ns}	9.546^{***}	4.321^{**}	
B. Nutr. extremes (grafts):						
plant source (df = 1,8)	1.726^{ns}	5.888^{**}	0.107^{ns}	0.998^{ns}		
treatment (df = 1,8)	44.723^{***}	20.780^{***}	73.000^{***}	0.431^{ns}		
interaction (df = 1,8)	1.774^{ns}	2.235^{ns}	0.126^{ns}	0.534^{ns}		
C. Excess phosphate:						
plant source (df = 1,32)	0.459^{ns}	9.609^{***}	0.401^{ns}	3.702^{*}	2.488^{ns}	3.392^{*}
treatment (df = 2,32)	0.288^{ns}	0.517^{ns}	0.614^{ns}	1.440^{ns}	0.326^{ns}	1.830^{ns}
interaction (df = 2,32)	0.832^{ns}	0.101^{ns}	0.065^{ns}	0.770^{ns}	0.012^{ns}	1.806^{ns}
D. Drought:						
plant source (df = 1,16)	0.557^{ns}	0.393^{ns}	0.477^{ns}	0.116^{ns}	0.219^{ns}	0.348^{ns}
treatment (df = 1,16)	21.291^{***}	23.799^{***}	127.765^{***}	1.445^{ns}	30.431^{***}	52.928^{***}
interaction (df = 1,16)	0.129^{ns}	0.471^{ns}	0.734^{ns}	2.363^{ns}	0.353^{ns}	0.127^{ns}
E. Waterlogging and salinity:						
plant source (df = 1,24)	0.232^{ns}	5.217^{**}	0.001^{ns}	1.252^{ns}	0.037^{ns}	0.377^{ns}
treatment (df = 2,24)	4.632^{**}	4.136^{**}	3.048^{*}	4.005^{**}	1.957^{ns}	0.809^{ns}
interaction (df = 2,24)	0.670^{ns}	0.104^{ns}	1.491^{ns}	0.122^{ns}	2.756^{*}	2.221^{ns}

[1] Plant source refers to whether seed (or cuttings) were collected from healthy or dieback trees; treatment details are shown in Table 1; mean values for each level of plant source & treatment are shown in Table 2.
*** P<0.01; ** P<0.05; * P<0.10; ns P>0.10.

Table 4. Effect of drought stress on volatile oil content of seedling foliage.

	Volatile oil content (% dry weight):											
	β-pinene			α-pinene			cineole			total		
	Mn	H	DB	Mn	H	DB	Mn	H	DB	Mn	H	DB
Mean	.30	.35	.26	.13	.10	.16	.42	.36	.47	.89	.88	.91
Well watered	.24	.33	.15	.09	.09	.08	.45	.45	.46	.83	.94	.72
Droughted	.37	.37	.37	.17	.12	.23	.38	.28	.48	.96	.83	1.09
F-Values:												
plant source (df = 1,16)	0.607^{ns}			2.029^{ns}			1.994^{ns}			0.024^{ns}		
treatment (df = 1,16)	1.287^{ns}			6.197^{**}			0.873^{ns}			0.676^{ns}		
interaction (df = 1,16)	0.526^{ns}			2.196^{ns}			1.509^{ns}			2.372^{ns}		

(Abbreviations & symbols as in previous tables).

Table 5. Chemical properties of topsoil at 10cm depth under groups of dieback-affected and healthy Eucalyptus blakelyi trees at Hall, in the Australian Capital Territory*.

location[1]	pH[2]	cond.[3]	%loi[4]	%total N[5]	%total P[5]	av.P[6]
A (db)	5.7 ±0.3	0.11 ±.03	13.5 ±1	.083 ±.02	.048 ±.003	24 ±3
B (db)	5.1 ±0.3	0.03 ±.03	8.5 ±1	.053 ±.02	.048 ±.003	18 ±3
C (heal)	5.3 ±0.3	0.04 ±.03	5.6 ±1	.018 ±.02	.046 ±.003	23 ±3
D (heal)	5.8 ±0.3	0.03 ±.03	5.7 ±1	.024 ±.02	.046 ±.003	19 ±3

1 db = group of dieback trees; heal = group of healthy trees. Number of soil samples collected from each group = 12

2 pH on 1:5 soil-water mixture

3 conductivity of 1:5 soil-water mixture ($\mu s\ cm^{-1}$)

4 % loss on ignition (after heating to 650°C for 1 hour)

5 Kjeldahl digest; autoanalyzer determination

6 molybdate-vanadate determination of phosphorus soluble in 0.1M hydrochloric & sulphuric acid (ppm).

* from a project by D.J. McGuire, N.D. Rowntree, and P.A. Williams for an undergraduate geography course on 'Soils and Vegetation Systems' taught by Dr. D.S. Gillieson at the Australian Defence Force Academy, Canberra, 1985.

FEEDING PREFERENCES OF COMMON BRUSHTAIL POSSUMS ON SEEDLINGS OF A WOODLAND EUCALYPT

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ABSTRACT

When Eucalyptus blakelyi seedlings were placed on platforms in the canopies of mature trees, common brushtail possums (Trichosurus vulpecula) selectively browsed on seedlings that had been irrigated with a balanced nutrient solution, in preference to other seedlings that had been irrigated with tapwater. The foliage of the nutrient-irrigated seedlings contained more water, nitrogen, soluble sugar and fibre, and less tannin, starch and non-structural carbohydrates, than did the foliage of the tapwater-irrigated plants. Its specific leaf weight was also lower. Although much more of the foliage on nutrient-irrigated plants was browsed, the possums also browsed foliage on some of the tapwater-irrigated plants. Within this treatment, the foliage of the plants preferred by the possums contained more sugar, less tannin, and less fibre than that of the less preferred plants. These data are discussed in terms of the dietary basis of feeding preferences of marsupial folivores.

INTRODUCTION

The common brushtail possum (Trichosurus vulpecula Kerr), like many other species of arboreal marsupials, displays a high degree of dietary selectivity (for examples see Smith & Hume 1984). Several studies (e.g. Cork & Pahl 1984; Fitzgerald 1978; Southwell 1978; Ullrey et al. 1981) have attempted to relate this selectivity to differences in the dietary composition of food plants, but have met with mixed success. Selectivity on the basis of dietary composition appears to be more consistent within a species of food plant, than between species. Cork and Pahl (1984) suggest this could be because differences other than dietary composition dominate when animals select between plant species. Most studies of the dietary basis of varying preferences for foliage from the same species of plant have been confined to comparisons of young and mature foliage (e.g. Cork & Pahl 1984), or to experiments with captive animals (e.g. Ullrey et al. 1981).

The causes of differences in dietary quality of leaves of similar age on the same species of tree are still largely undetermined. Studies with herbivorous insects have implicated both genetic and environmental components of intraspecific variation in the quality of leaves as food for herbivorous insects (e.g. Denno & McClure 1983).

I conducted a field experiment involving seedlings of Eucalyptus blakelyi Maiden from two different seed sources (genetic component), grown under two different nutrient regimes (environmental component) which was designed to test theories relating to insect herbivory (Landsberg submitted d). Dietary quality of the seedlings was measured, and they were placed on platforms in the canopies of mature trees for nearly seven weeks. The experiment was terminated because common brushtail possums selectively ate most of some plants while hardly touching other plants on the same platforms. The basis of this selectivity in terms of dietary composition of the seedlings' foliage is described here.

METHODS

ORIGINAL AIM OF THE EXPERIMENT

Dieback of native trees on farms is becoming increasingly common in many regions of Australia (Kile 1981). In remnants of native woodland on pastoral properties in the Australian Capital Territory, dieback of one of the common tree species, E. blakelyi, is associated with defoliation by herbivorous insects (Landsberg submitted b). Trees with dieback tend to be more heavily grazed by insects than healthier trees nearby, and their foliage tends to be nutritionally superior for insects (Landsberg submitted c).

This experiment was designed partly to investigate the relative importance of genetic background and growing conditions in determining the dietary quality of foliage of seedlings of E. blakelyi. Secondly, I wanted to test whether seedlings which differed in the dietary quality of their foliage would sustain different amounts of grazing by the insects present in the canopies of mature trees, under field conditions.

SEEDLINGS

Seed for the experiment was collected from two isolated stands of E. blakelyi trees growing on pastoral properties near Hall, in the Australian Capital Territory. All the trees in one of the stands had dieback; the trees in the other stand all appeared healthy. Seedlings were initially grown in a glasshouse, in large, freely-draining pots containing a sand-vermiculite-pearlite mixture, and were irrigated frequently with a balanced nutrient solution containing 5 mM nitrogen (Landsberg submitted d; modified from Ingestad 1971).

When they were 30-40 cm tall, matched pairs of 'h' (healthy seed source) and 'db' (dieback seed source) plants were randomly assigned to either 'nutrient' or 'water' irrigation treatments. Plants in the nutrient treatment continued to be irrigated with the nutrient solution, but water treatment plants were irrigated with tapwater only, for the rest of the experiment. Each pair of potted 'h' and

'db' seedlings was placed in an opaque plastic box, to give 24 nutrient treatment and 24 water treatment boxes, each containing a matched pair of seedlings. The boxes were fitted with styrofoam lids through which the seedlings' stems protruded, and were transferred to open-air, partially shaded benches. The irrigation treatments were continued via plastic inlet tubes, and drainage occurred through outlet tubes set about 5 cm above the bases of the boxes.

THE FIELD EXPERIMENT

The experiment was conducted during summer, from 3 January to 19 February 1985, in remnant woodland on a pastoral property near Hall. The site is a semi-cleared woodlot on a gentle hillslope with some rock outcrop; the pasture is dominated by Phalaris sp., and grazed by cattle and sheep. The dominant tree species is E. blakelyi, with scattered individuals of E. melliodora A. Cunn. ex Schau. and E. macrorhyncha F. Muell. ex Benth. also present. The condition of the trees' canopies varies widely; some appear healthy and others show varying degrees of dieback.

Three years before the experiment began, poles fitted with platforms had been positioned adjacent to six mature E. blakelyi trees (heights ranged from 10 to 15 m) at the study site, such that the platforms projected into the trees' canopies. Three of the trees were healthy, and three had dieback. The platforms were partially protected from the wind by a 0.8 m high shade cloth fence which surrounded three sides of each platform. Four of the boxes of seedlings (two nutrient treatment boxes and two water treatment ones) were placed on each canopy platform, using a travel tower for access. The seedlings had been receiving different irrigation treatments for the previous 10 weeks, and the larger plants were 70-80 cm tall. By this time the water treatment seedlings were significantly smaller than the nutrient treatment plants (63.8 cm compared with 71.3 cm; $t=2.1$, $df=22$, $P<0.05$). However as the seedlings on the platforms continued to grow, their foliage became intermingled. Daily irrigation was continued, with solutions being pumped from the ground through hoses fitted to the inlet tubes.

I checked the condition of the seedlings at least weekly, by climbing the poles, which were fitted with climbing spikes. I noted possum scat on one of the platforms, and possum damage to several of the seedlings on it, in the first week. Thereafter I set cage traps each evening, and I trapped and removed six common brushtail possums during the course of the experiment. Possums caused little damage after the first week, until the seventh week, when several plants on four of the platforms were severely damaged, and I discontinued the experiment.

DIETARY QUALITY OF SEEDLING FOLIAGE

I measured a range of variables associated with dietary quality, on foliage samples collected in the week prior to the commencement of the field experiment. The samples consisted of 50-100 discs of known area cut from each of three age classes of leaves (young, nearly mature, mature) on each seedling. These were collected from before dawn till one hour after dawn, to minimize differences caused by diurnal variations in leaf properties. They were frozen in liquid nitrogen immediately after collection, then stored in liquid nitrogen until they could be weighed, then freeze-dried and re-weighed, after which they were ground to a powder. This was stored at $-15^{o}C$ in stoppered vials above a desiccant until it could be analyzed, up to 9 months later.

The methods of analysis of dietary quality variables are described more fully elsewhere (Landsberg submitted c). The variables measured were: water content (per fresh weight of leaf); specific leaf weight (dry weight per unit area); content of total soluble sugars total non-structural carbohydrates and starch (glucose specific assay following enzymatic hydrolysis, Azcon-Bieto & Osmond 1983); total nitrogen content (Technicon auto-analyzer determination on micro-Kjeldahl digest); and tannin content (relative astringency in a haemoglobin solution against a tannic acid standard, Schultz et al. 1981). Volatile oils were measured by gas chromatography, and major constituents were verified by co-injection with reference compounds.

There was insufficient leaf material to perform all assays on all samples. Water content, specific weight and total nitrogen were measured for all age classes of leaves, the carbohydrate measures and volatile oil determinations were made on 'nearly mature' leaves only, and tannin concentration was measured on 'young' leaves only. Most of the 'mature' foliage, which consisted of early seedling leaves, abscissed soon after the plants were placed in the canopies, and so was not eaten by the possums or analysed for other than N and water content.

Fibre content is often low in the preferred diet of ringtail possums (Pseudocheirus peregrinus; Cork and Pahl 1984) and koalas (Phascolarctos cinereus; Ullrey et al. 1981), and could therefore be important in determining feeding preferences of common brushtail possums, as could leaf toughness. Since these aspects of dietary quality had not been assessed before the field experiment, I measured them on a subsample of seedlings at the end of the experiment. The subsample consisted of the plants in four water treatment and four nutrient treatment boxes from the two platforms which had escaped major damage by possums. I sampled little-damaged mature leaves from this subsample, as described earlier, and measured their neutral-detergent fibre content (Cork & Pahl 1984), and their specific leaf weights and water content. I also measured the toughness of similar, intact leaves on the same plants, using a simple penetrometer (Lowman & Box 1983), with a 3 mm diameter cutting rod.

ASSESSMENT OF DAMAGE CAUSED BY POSSUMS

Possums tear and chew leaves, petioles and stems, causing a pattern of damage which is easily distinguished from that caused by insect feeding. I measured the extent of the damage caused by possums by estimating, for each seedling, the total length of stems on which most of the leaves had been severely damaged, and expressing this as a proportion of the total length of all stems on that seedling. There was little point in attempting a more precise measure of damage (e.g. leaf area missing), since insects had also been feeding on the leaves. Thus an unknown proportion of each leaf damaged by possums may have been previously damaged by insects. Even in the absence of insect

feeding, the actual area of leaf missing could only be roughly estimated, since the possums removed most of the soft tissue from each leaf they damaged.

The data on possum damage and dietary quality were analyzed using the analysis of variance subroutines from the Genstat computer program (Alvey et al. 1982).

RESULTS

DAMAGE BY POSSUMS

Seedlings that had been irrigated with nutrient solution sustained significantly more damage from possums than those that had been irrigated with tapwater only (Tables 1 & 2). On average, about half of their stems had been damaged (Table 2; 0.53 mean proportional stem damage), regardless of the source of their seed or the health of the mature tree canopy in which they were placed. There was also a significant interaction between the irrigation treatments and seed source, although this did not explain as much of the variance as did the effect of the irrigation treatments alone (Table 1). Overall, the possums mainly chose to eat nutrient-irrigated seedlings. However, when they did eat water-irrigated plants, they appeared to prefer those from the healthy seed source (Table 2; 0.27 of healthy-source stems damaged, compared with 0.14 of the stems of the dieback-source plants).

DIETARY QUALITY OF SEEDLING FOLIAGE

Leaves of seedlings irrigated with nutrient solution were, in general, nutritionally superior to those from plants irrigated with tapwater. On average they contained more water, more total nitrogen, more soluble sugars, and less tannin (Table 3). They also tended to be thinner (lower specific leaf weight), which might have partially resulted from lower concentrations of non-structural carbohydrates and starch (Table 3).

In contrast, the concentration of neutral-detergent fibre was also higher in the nutrient-irrigated plants (Table 3), although high fibre content is often associated with lowered dietary quality (van Soest 1977). However, since I measured the fibre content of only a subsample of plants at the end of the experiment, these data may not adequately represent the possums' feeding preferences. Rather surprisingly, the fibre contents were negatively correlated with the specific leaf weights of the same samples (Pearson's $r = -0.70$; $P<0.01$). This suggests that, for these subsamples, a high concentration of cell-wall constituents (of which neutral-detergent fibre is an index), did not result in thicker leaves.

Leaf toughness was highly variable. The mean weight required for penetration of a leaf by the penetrometer rod, averaged over all 16 plants, was 267 gm, with a standard deviation of 50 gm. However, the average coefficient of variation (std.dev. / mean x 100%) for measures of different leaves on the same seedling (30%) was considerably higher than the coefficient of variation between the seedlings, which was 19%. The average coefficient of variation for readings taken on the same leaf was even higher at 36%. Few of the leaves were completely undamaged, and this may have contributed to the variation within leaves. As with the fibre values, there are difficulties with interpreting the biological significance of these retrospective measures.

If the fibre contents or toughness of leaves in the subsample were highly correlated with their water contents or specific leaf weights, this would allow some inferences to be made about the probable fibre content or toughness of the larger sample of plants. Significant correlations occurred between between fibre content and specific leaf weight (referred to earlier), between fibre and water contents (Pearson's $r = 0.62$; $P<0.05$), and between toughness and water content (Pearson's $r = 0.46$; $P<0.10$). However, regressions between these pairs of correlated variables explained too little of their variance (<20%) to justify their use for extrapolation to the larger sample.

The concentration of volatile oils did not differ significantly between the experimental treatments. The average concentration of volatile oils in leaves was 0.93% (dry weight), of which over half was cineole (mean cineole concentration = 0.59%) and much of the remainder was β pinene (mean = 0.25%).

Seed source did not contribute significantly to variation in many of the dietary quality variables measured (Table 3). The concentration of soluble sugars was higher for seedlings from the healthy seed source and the fibre content was lower. In addition, the young leaves of nutrient-irrigated 'h' seedlings contained more water, and those of the water-irrigated 'h' seedlings contained less tannin. Thus the few dietary quality variables which differed with seed source tended to enhance the dietary quality of the seedlings derived from healthy, rather than dieback, trees.

There were consistent trends in the effect of leaf age on those variables for which information is available. As leaves aged their water contents decreased and their specific weights increased. Nitrogen content decreased from young to nearly mature leaves, but nearly mature and mature leaves had the same nitrogen concentrations (Table 3).

DISCUSSION

The possums in this experiment selectively fed on seedlings grown under a high nutrient regime, regardless of the source of the seed or the vitality of the tree canopy in which the seedlings were placed. The foliage of these preferred seedlings was also nutritionally superior to that of the less preferred seedlings, in terms of many of the dietary variables I measured. Thus these possums were able to distinguish between plants of relatively high dietary quality and very similar plants of lower quality, even when the foliage of these plants was intermingled.

Captive koalas were also able to distinguish nutritionally superior foliage, and preferred to browse on it (Ullrey *et al*. 1981).

Degabriele (1983) has suggested that the proximate basis of food selection by koalas may be avoidance of foliage with a high fibre content, and that this will usually correlate with selection for high nitrogen content. Low foliar fibre was not a good indication of high foliar nitrogen in my experiment, although my fibre data are problematic. However the possums' preference (within the water irrigation treatment) for healthy-source seedlings over dieback-source ones is suggestive, in terms of the proximate basis for their selection. These plants differed only in their contents of sugars, tannins and fibre, and only the differences in sugars and tannins were also consistent with the possums' major preference for nutrient-irrigated plants. Within both irrigation treatments, the possums consistently fed on sweeter and less astringent foliage. This accords well with Bate-Smith's (1972) suggestion that sweetness may be a universal attractant in determining food preferences of higher animals, and that astringency may be a powerful repellent.

If either sweetness or low astringency is generally correlated with nutritionally favourable foliage, then folivores would tend to optimize their nutritional uptake by selecting on this proximate basis. The photosynthetic capacity of leaves is closely linked with their nitrogen content (Mooney & Gulmon 1982). Thus, in general, foliage with a high nitrogen content will also be likely to contain a high concentration of photosynthates such as soluble sugars. In general, too, deficiencies of plant nutrients such as nitrogen often tend to result in high concentrations of phenolic substances such as tannins (Gershenzon 1983). Unfortunately changes in the composition of foliage as it ages complicate these relationships. For mature E. blakelyi trees during two growing seasons, the average concentrations of foliar nitrogen and tannin tended to be negatively correlated (Landsberg submitted c). However the concentrations of nitrogen and tannins were both at their highest in young foliage, which was also the preferred diet of insect herbivores. Similarly Cork and Pahl (1984) found that the young foliage generally preferred by ringtail possums also had relatively high concentrations of both nitrogen and tannins.

Neither total yield of volatile oils nor the composition of the oil influenced the preferences of common brushtail possums for particular seedlings. Similarly, Southwell (1978) also found that the feeding preferences of koalas were unrelated to the yield or composition of oils in the foliage of a large number of their potential food trees. These results question some of the earlier assumptions (eg Eberhard 1978, for koalas, and Freeland and Winter 1975 for common brushtail possums) about the importance of oils in the diet of marsupials that feed on eucalypt foliage.

The possums' preference, among the water-irrigated plants, for plants from the healthy seed source is also interesting in terms of genetic predisposition to herbivory. Dieback-affected adult trees experience most insect damage. Therefore I had expected that, if there was a genetic predisposition to herbivory for some of the seedlings, it would have been expressed as higher damage on seedlings from dieback trees. Instead, possums selected for seedlings from healthy trees. Although I have no information available about whether insects showed similar preferences, this result for the possums raises interesting questions about which seedlings, if any, may have been preferentially grazed by insects, and about how important genetic predisposition is in determining susceptibility to dieback.

The differences in leaf properties between nutrient-irrigated and tapwater-irrigated plants were probably the result of differences in the balance of supply of carbon and nitrogen. My results are very similar to those of Waring et al. (1985), who found that plants grown with a high nutrient supply had high concentrations of nitrate, amino acids and total nitrogen. In contrast, plants grown with a more moderate nutrient supply had a relative surplus of carbon. These plants, like my tapwater-irrigated ones, accumulated relatively high concentrations of starch and tannins, and had high specific leaf weights. Waring et al. found that the increased nitrogen content in leaves with high nutrient supply was associated with higher rates of photosynthesis per unit of biomass, but not per unit of leaf area. The tapwater-irrigated plants in my experiment may also have had photosynthetic rates per unit area that were comparable with those of the nutrient-irrigated plants, but their restricted nitrogen supply may have limited rates of conversion of photosynthate to amino acids.

Thus proportionately more of their photosynthate would be converted to storage products such as starch, and secondary compounds such as tannins, which were both present in high concentrations in the nutrient-limited plants.

Many of my conclusions regarding the feeding preferences of possums are speculative, especially since I have so little information about the possums that caused the damage I recorded. Further, my results relate to a relatively short interval in the dynamic environment of the animals, in terms of both tree phenologies and animal physiology. Nevertheless these animals showed a very discerning preference for browsing on nutrient-rich seedlings. The dietary composition of these seedlings offers some interesting clues about the basis of this preference.

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Table 1. Summary analysis of variance for possum feeding damage

Source of variation	df	ss	ss%	ms	variance ratio
Tree stratum					
canopy health	1	0.0001	0.00	0.00001	0.000
residual	4	3.04499	57.55	0.76125	
Total	5	3.04500	57.55	0.60900	
Tree x box stratum					
irrigation	1	1.22509	23.16	1.22509	59.884***
canopy health x irrigation	1	0.00167	0.03	0.00167	0.082
residual	16	0.32733	6.19	0.02046	
Total	18	1.55409	29.37	0.08634	
Tree x box x pot stratum					
seed source	1	0.02497	0.47	0.02497	1.050
canopy health x seed source	1	0.00707	0.13	0.00707	0.297
seed source x irrigation	1	0.10085	1.91	0.10085	4.439**
canopy health x seed source x irrigation	1	0.08290	1.57	0.08290	3.484
residual	20	0.47583	8.99	0.02379	
Total	24	0.69162	13.07	0.2882	
Grand total	47	5.29071	100.00		

Grand mean = 0.365 Total number of observations = 48 *** P<.01 ** P<.05

Table 2. Table of mean values for treatments which contributed significantly to the variance in possum feeding damage (expressed as mean proportional stem damage).

Age of leaves[1]	Significant treatment[2]	Variance ratio[2]	Means[3] by seed source[4] h	db	irrigation tmt.[5] nutr.		water	SED (reps)[6]
all ages	irrigation	59.88 (1,16)***	h & db		0.53	***	0.21	0.04 (24)
	irrig'n x seed source	4.44 (1,20)**	h		0.50	***	0.27	
					ns		**	0.06 (12)
				db	0.55	***	0.14	

[1] Leaf ages refer to leaves sampled prior to seedlings being placed on platforms (Dec 84-Jan 85), except when labelled (Feb 85), which refers to leaves sampled at the end of the experiment.

[2] From summary analysis of variance (Table 1): *** P<0.01, ** P<0.05, ns P>0.05

[3] Mean values for each level of significant treatments, indicating which means differed significantly. Significance determined from $t = (mean_1 - mean_2) / SED$ (df = residual df from vr).

[4] h refers to mean values for healthy seed source; db to means for the dieback seed source; h & db refers to combined means for seed from both sources.

[5] nutr. refers to mean values for the nutrient-irrigated treatment; water to means for the water-irrigated treatment; nutr. & water refers to combined means for both treatments.

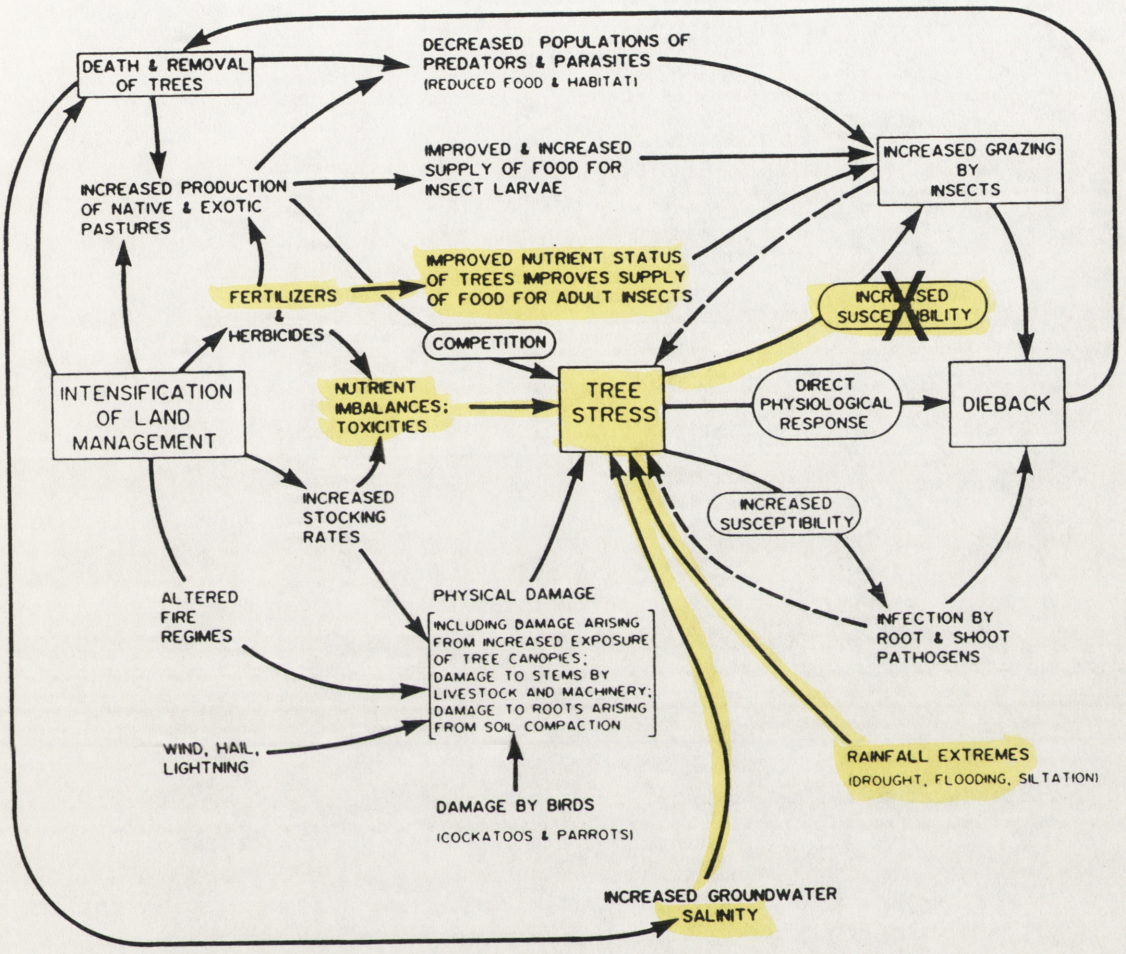
[5] SED is the standard error of difference of the means. (reps) is the number of replicates.

Table 3. Summary table of mean values for treatments which contributed significantly to the variance in dietary quality variables. Significant treatments were determined from ANOVA, as illustrated in Tables 1 & 2.

Age of leaves	Significant treatments	Variance ratio (df)	Means by seed source		irrigation tmt.			SED (reps)
			h	db	nutr.		water	
A. Water content:								
young	irrigation	36.53 (1,16)***	h & db		73.8	***	69.7	0.7 (24)
	irrig'n x		h		74.8	***	69.4	
	seed source	5.79 (1,18)**			**		ns	0.9 (12)
				db	72.9	***	70.0	
nearly mature	irrigation	23.11 (1,16)***	h & db		71.4	***	66.9	0.9 (24)
mature (Jan 85)	irrigation	26.73 (1,16)***	h & db		70.7	***	63.8	1.3 (24)
mature (Feb 85)	irrigation	5.98 (1, 6)**	h & db		67.3	**	63.8	1.4 (8)
B. Specific leaf weight:								
young	irrigation	44.83 (1,16)***	h & db		5.18	***	6.55	0.02 (24)
nearly mature	irrigation	26.16 (1,16)***	h & db		5.51	***	6.66	0.02 (24)
mature (Jan 85)	irrigation	25.54 (1,16)***	h & db		5.93	***	7.46	0.03 (24)
mature (Feb 85)	irrigation	22.58 (1,6)**	h & db		7.4	***	9.4	0.4 (8)
C. Total nitrogen:								
young	irrigation	298.56 (1,16)***	h & db		3.80	***	1.42	0.14 (24)
nearly mature	irrigation	158.10 (1,16)***	h & db		3.29	***	1.30	0.16 (24)
mature (Jan 85)	irrigation	357.28 (1,16)***	h & db		3.26	***	1.30	0.10 (24)
D. Total soluble sugars:								
nearly mature	irrigation	61.18 (1,16)***			6.20	***	3.70	0.32 (24)
	seed source	4.67 (1,14)**	5.26 (h)		nutr. & water			
			**					0.29 (24)
				4.64 (db)	nutr. & water			
E. Total non-structural carbohydrates:								
nearly mature	irrigation	8.20 (1.12)**	h & db		10.5	***	14.9	1.5 (24)
F. Starch:								
nearly mature	irrigation	16.22 (1,12)***	h & db		4.5	***	11.0	1.6 (24)
G. Tannins:								
young	irrigation	16.34 (1,15)***	h & db		20.9	***	30.4	2.4 (24)
	irrig'n x		h		22.0	**	27.4	
	seed source	8.15 (1,16)**			ns		***	2.8 (12)
				db	19.7	***	33.3	
H. Neutral-detergent fibre:								
mature (Feb 85)	irrigation	16.59 (1,6)***	h & db		45.4	***	38.1	1.8 (8)
	seed source	5.93 (1,6)**	39.8 (h)		nutr. & water			
			**					1.7 (8)
				43.7 (db)	nutr. & water			

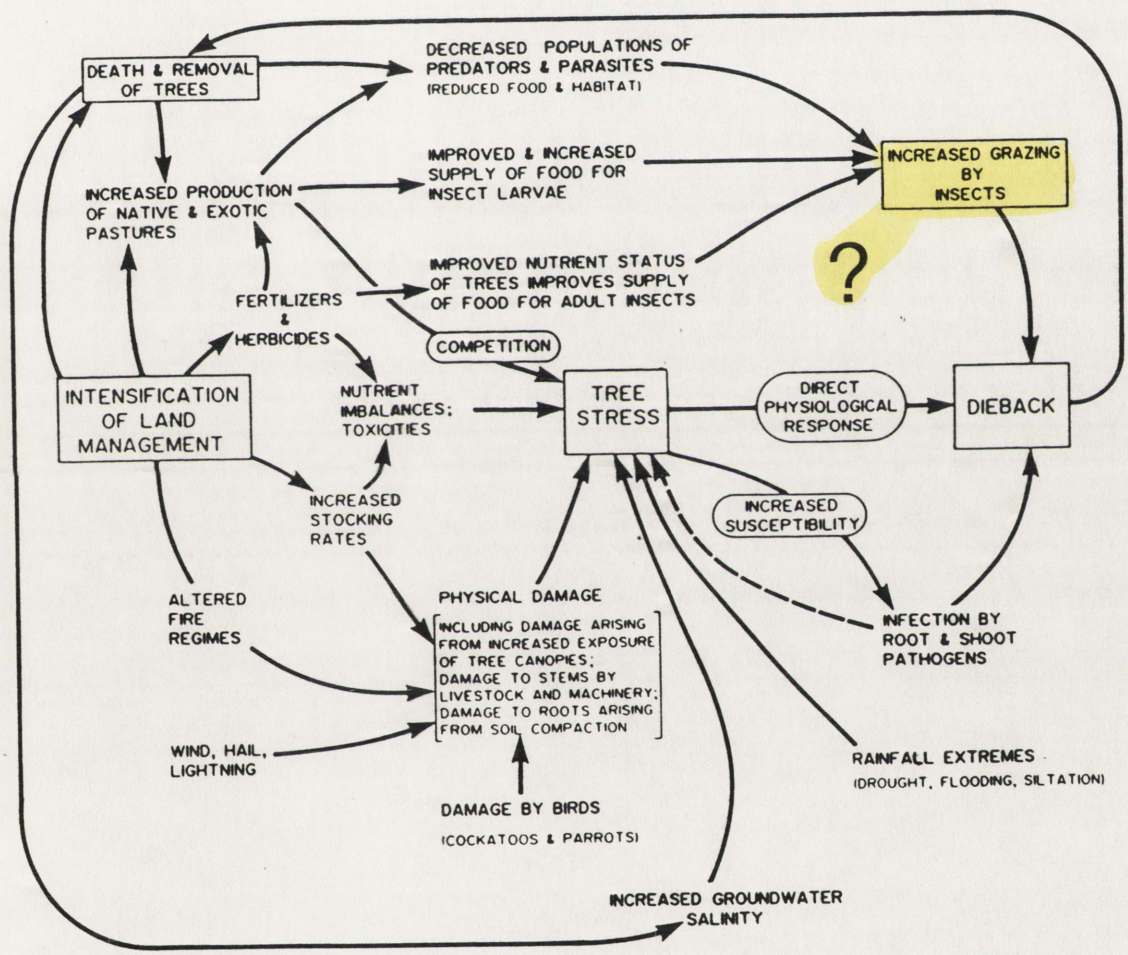
For explanation of column headings see Table 2

Water content is expressed as % fresh weight; specific leaf weight as $mg.cm^{-2}$; total nitrogen as % freeze-dried weight; soluble sugars, carbohydrates and starch as % freeze-dried weight of glucose equivalents; tannins as % freeze-dried weight of tannic acid equivalents; neutral-detergent fibre as % freeze-dried weight.



Drought reduced the dietary quality of the foliage of dieback and healthy trees, and subsequent insect grazing on it. Several kinds of environmental stress also reduced the dietary quality of the foliage of seedlings derived from dieback and healthy trees. Benign growing conditions enhanced dietary quality of foliage. Herbivorous possums selectively browsed on nutritionally favourable foliage, but the preferences of herbivorous insects were not determined.

What is the effect of defoliation on the dietary quality of foliage and subsequent insect grazing on it?



SUSCEPTIBILITY OF EUCALYPT TREES TO GRAZING BY INSECTS: RESPONSE TO DEFOLIATION

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ABSTRACT

Eucalypt trees readily produce replacement epicormic foliage after defoliation of their primary canopies. The foliage that regrew on eucalypts I had artificially defoliated was nutritionally superior to the foliage it replaced, and was much more heavily damaged by grazing insects. There was a transient increase in the tannin content of the regrowth foliage, but this was apparently ineffective in defending it from subsequent herbivory. The regrowth foliage was also nutritionally superior to and more damaged than the foliage on nearby trees that produced major flushes of leaf growth during the same period. Some of these nearby trees were suffering canopy dieback associated with chronic high levels of insect grazing, and other healthier trees were more resistant to damage from insects. The dietary quality of the regrowth foliage was more similar to that of the foliage on the dieback, rather than the healthy trees. Trees such as eucalypts that have high capacities for compensatory growth, and that lack effective induced defences against herbivory, are at risk from 'resource regulation' by their insect herbivores whenever other controls on insect populations are reduced. Canopy dieback may develop if trees' capacity for compensatory growth is also reduced, such that recovery is not sufficient to compensate for foliage loss.

INTRODUCTION

Compensatory growth responses of many plants after defoliation result in rapid replacement of lost photosynthetic capacity and thus alleviate many of the potentially damaging consequences of herbivory. Compensatory growth is possible when environmental or physiological changes following defoliation result in enhanced nutrient and water status and rates of photosynthesis in surviving and regrowth foliage (McNaughton 1983).

There are, however, costs associated with the benefits of compensatory growth. Rapid replacement of damaged tissue is achieved, in part, by depletion of plant reserves, and the impact of this on subsequent plant fitness depends on the timing, severity and frequency of defoliation (e.g. Ericsson et al. 1980). In addition the enhanced photosynthetic rates of compensatory growth may increase the risk of subsequent herbivory, because both photosynthetic capacity and herbivory depend on the nitrogen content of foliage (Mooney & Gulmon 1982).

This risk may be minimized if defoliation also induces effective physical or chemical defences against further herbivory. Induced plant defences have been shown to decrease insect fitness in a number of laboratory-based studies (e.g. Haukioja & Niemela 1979; Haukioja & Hanhimaki 1985; Raupp & Denno 1984; Wratten et al. 1984). However, unequivocal demonstrations of damage-induced plant defences having a major effect on populations of insects in the field are extremely rare (see Fowler & Lawton 1985). Declines in insect populations subsequent to heavy defoliations of their tree hosts do occur, but are as likely to result from passive deterioration of the insects' food resource as from active production of chemical defences (e.g. Baltensweiler et al. 1977; Valentine et al. 1983).

If plants lack effective defences, then insects may be able to achieve 'resource regulation', whereby a high quality regrowth resource is maintained by successive defoliation cycles (Craig et al. 1986).

Bryant et al. (1983) have developed an hypothesis to explain when it may be most advantageous to plants to produce effective defences against herbivory. They suggest that selection for rapid compensatory growth or for effective chemical defence will depend on plants' intrinsic growth rates, which are constrained by the availability of resources. Thus plants adapted to high resource environments will have a greater capacity for compensatory growth and are likely to be chemically defended only in the more susceptible juvenile phase, in contrast to low-resource-adapted plants, which are more likely to have well developed defences throughout their lives.

Eucalypt trees provide an interesting test of this theory. They occur in environments which are generally nutrient poor (Bowen 1981) and their canopies are commonly grazed by many different species of insects (though the actual extent of the damage they cause is controversial - see Fox & Morrow 1983 and Ohmart 1984). In addition most species of eucalypts are especially well adapted to defoliation, in that, in response to partial or complete loss of their primary canopies, they readily produce replacement epicormic foliage from dormant bud strands which are abundant in their stems and branches (Jacobs 1955). This epicormic foliage is juvenile in form, and differs both morphologically and physiologically from adult-form foliage (Blake 1980; Jacobs 1955). Thus from Bryant et al.'s hypothesis it follows that the foliage of eucalypts should be well defended against herbivory, possibly throughout their life spans because growth rates may be constrained by a limited nutrient supply, but particularly when the foliage is juvenile in form, as when epicormic foliage is produced following defoliation.

However there are a number of indications that this may not be so. Larvae of the eucalypt-defoliating sawfly Perga affinis affinis regulate their food resource by repeatedly grazing on the foliage produced after previous defoliations (Carne 1965). In addition eucalypt dieback is becoming increasingly common in many parts of rural Australia (Kile 1981). Trees develop dieback after repeated cycles of canopy loss and replacement, yet trees with dieback are often more heavily grazed by insects than are nearby healthy trees (Landsberg submitted b). Although the dietary quality of the foliage of dieback trees is often more favourable for insects than that of

neighbouring healthy trees, the extent to which this is a cause or a consequence of defoliation is unclear (Landsberg submitted c).

Healthy eucalypts may remain so, in part at least, because they are well defended from, or nutritionally inadequate for, insect herbivores, and trees may develop dieback because they are genetically or environmentally predisposed to be less well defended or more nutritious. Alternatively eucalypts may be generally adapted to maximize compensatory growth following defoliation, and, if effective defences are lacking, they may therefore be at risk from resource regulation by their insect herbivores. This second alternative appears maladaptive, if insect grazing has exerted a strong selective pressure on evolution of eucalypts. Yet it appears to describe the interaction between sawfly larvae and their eucalypt hosts (Carne 1965), and may therefore also apply to other eucalypt-insect systems.

I investigated whether this was so for a species of eucalypt which is very susceptible to 'rural tree dieback'. I artificially defoliated three previously healthy trees and followed changes in the dietary quality of their regrowth foliage and insect herbivory on it, while concurrently monitoring these parameters on nearby healthy trees and trees suffering from dieback.

METHODS

STUDY SITES AND TREES

Eucalyptus blakelyi Maiden is a woodland eucalypt that occurs extensively on the pastoral lands of the slopes and tablelands of south eastern Australia (Milton Moore 1975), and is very susceptible to rural tree dieback (Duggin 1981). I studied mature E. blakelyi trees (average height 10-12m) growing on a pastoral property near Hall, in the Australian Capital Territory. The property is managed for grazing of sheep and cattle, and the trees, whose apparent vigour varies markedly, are remnants of the original natural woodland retained for shade and shelter. I classified them as 'healthy' or 'dieback' from an assessment of the size and density of their crowns

and the extent of epicormic growth and branch death; the foliage of the dieback trees was generally more heavily grazed by insects (Landsberg submitted b). I monitored five dieback trees and eight healthy trees from early September 1983 to September 1984.

I artificially defoliated three of the healthy trees in mid-September 1983, prior to the late spring growth flush, by clipping most of their terminal branchlets (diameter <1cm) using hand clippers, and gaining access from ladders and a travel tower. One leading branch (100-200 leaves) was retained on each tree, to reduce any chance of mortality (Blake 1981).

HERBIVORY AND DIETARY QUALITY

The extent of damage caused by insects, and foliar dietary quality, were assessed on foliage samples of about 100 leaves per tree. These were cut from the study trees before dawn, to minimize variation due to diurnal fluctuations in dietary quality. Methods of sampling and analysis are described more fully elsewhere (Landsberg submitted b & d).

Briefly: each sample was sorted into age (young, nearly mature, mature 1 & 2, old 1 & 2) and form (epicormic, intermediate 1-3, adult) categories, and dietary quality was assessed on discs cut from the leaves in each category. The extent of insect damage on the leaves in each category was estimated visually into nominal classes (none, a little, about an eighth, etc.), which were later calibrated against instrumented measurements. Damage was recorded as the proportion of foliar area removed, mined or skeletonized, necrotic, or covered by psyllids or galls (Landsberg submitted b).

Dietary quality variables measured were: water content (per fresh weight of leaf), specific leaf weight (weight per area), content of total soluble sugars (glucose specific assay following enzymatic hydrolysis; Azcon-Bieto & Osmond 1983), total nitrogen content (Technicon auto-analyzer determination on micro-Kjeldahl digest), and tannin content (relative astringency in a haemoglobin solution, against a tannin acid standard; Schultz et al. 1981) (Landsberg

submitted c). Concentrations of soluble sugars and tannins were measured only during the main growing period, until late autumn 1984.

STATISTICAL ANALYSES

These data were summarized for healthy, dieback and defoliated trees on each sampling date, as 'unadjusted means' (Tables 1-6), calculated from mean values for the samples from each tree, regardless of the age and form categories represented, and as 'adjusted means' (Tables 1-6), calculated from fitted statistical models. This adjusted the mean values for the trees to account for any significant variation amongst them that resulted from the effects of differences in the age or form of their leaves, or interactions between these and the condition of their canopies ('significant model terms' in Tables 1-6). In this way the significance of differences among the trees could be assessed, after adjusting for the effects of these factors. The significance of differences amongst the healthy, dieback and defoliated trees for both sets of mean values was then tested by 1-way analysis of variance (Alvey et al. 1982; Landsberg submitted b).

RESULTS

TREE GROWTH

The trees which had been artificially defoliated resprouted prolifically from epicormic buds along their major branches, from early November (the first shoots appeared two weeks after the pruning) till early January. During the same period other trees at the site also produced major leaf flushes and turned over about three quarters of their canopies (Landsberg submitted b). The regrowth leaves on the defoliated trees were intermediate in form, having neither the lanceolate shape of the adult-form leaves typical of healthy trees, nor the ovate shape of the juvenile-form epicormic leaves typical of dieback trees.

HERBIVORY

The proportion of foliar area mined or skeletonized, or covered by psyllids or galls, did not differ significantly among the groups of trees and was never greater than 1%. Necrosis was also a relatively minor form of damage, and seldom differed significantly among the trees.

Removal of foliar area was the most common form of damage (Table 1). Before any trees were artificially defoliated (September 1983) the dieback trees' foliage had a significantly greater proportion of its area removed than that of the healthy trees, including those which were subsequently defoliated. Much of this difference was due to variations among the trees in the age and form of their foliage. Once the trees' mean values had been adjusted to equalize the effect of these factors they were no longer statistically different.

There was no significant difference in the proportion of foliar area removed between any of the groups of trees shortly after the artificial defoliations (November 1983). However the samples from the artificially defoliated trees consisted of young leaves only, while the samples from the other trees also contained older leaves. Since damage tends to accumulate as leaves age, young leaves are generally less damaged than older leaves (Landsberg submitted b), and variation due to leaf age contributed significantly to the variation among trees (Table 1). When the trees' mean values were adjusted to equalize the effects of leaf age differences the adjusted values for the mean foliar area removed from both the dieback trees and the defoliated trees were significantly higher than that from the healthy trees.

This trend continued for the rest of the year, with the foliage from both defoliated and dieback trees accumulating significantly more damage than the foliage from the healthy trees (Table 1). By the end of the growing season (after March 1984) this difference was no longer a function of differences among trees in the age or form of their leaves. Towards the end of the year of monitoring (August and September 1984) the proportion of foliar area which insects had removed from the artificially defoliated trees was significantly more than that removed from either healthy or dieback trees, although the

dieback trees' foliage was still consistently more damaged than that of the healthy trees (Table 1).

At the end of the year of monitoring (September 1984) the foliage from the healthy trees was a little less damaged by insects than the foliage from these trees had been a year earlier, and the foliage from the dieback trees was a little more damaged (Table 1). In contrast the regrowth foliage on the artificially defoliated trees was damaged nearly three times as heavily as the foliage it replaced had been the year before.

DIETARY QUALITY

Before the three trees were artificially defoliated the foliage of the groups of trees differed only in its specific weight: dieback trees' leaves weighed less per unit area than those of healthy trees, a trend which was maintained throughout the study (Table 2). Although differences between healthy and dieback trees for the other quality variables were seldom significant, there were consistent trends. The dieback trees' foliage tended to have more nitrogen (Table 3), less soluble sugar (Table 4) and a higher water content (Table 5). However the tannin content of both groups of trees was similar (Table 6). Similar trends were recorded from September 1982 to September 1983 when more trees had been monitored for another study and during that time differences had often been significant (Landsberg submitted c).

The foliage which regrew on the artificially defoliated trees also had lower specific leaf weights and higher nitrogen contents than the foliage from healthy trees (Tables 2 & 3), and, during the first part of the study, tended to have higher contents of water and tannin (Tables 5 and 6). Shortly after the defoliation the regrowth foliage also had less soluble sugar than the foliage from healthy trees, but this difference was short lived (Table 4). Leaf age contributed to many of these differences, but when means were adjusted for leaf age the same trends remained.

DISCUSSION

Clearly the artificial defoliation of the eucalypts in this study increased the susceptibility of their replacement foliage to herbivory. Therefore the relatively high rates of herbivory on dieback trees may also derive, in part at least, from their history of repeated defoliations. Both the regrowth on the artificially defoliated trees and the foliage on the dieback trees showed many of the features of compensatory growth. Enhanced nitrogen and water status of the foliage and reduced specific leaf weights (resulting in a greater surface area of photosynthetic tissue per unit of biomass) suggest that rates of photosynthesis and therefore growth rates may also have been enhanced. Blake (1980) found that the juvenile foliage which coppiced from decapitated eucalypt seedlings had higher rates of stomatal diffusion and grew more quickly than the more adult-form foliage it replaced. The transient decrease in soluble sugar content which I measured in the regrowth foliage and the relatively low sugar content of the dieback trees' foliage suggest that this compensatory growth may be at the cost of some depletion of reserves (see also Bamber & Humphreys 1965). Similar changes in foliar properties after defoliation have been reported for several other tree species (e.g. red oak and red maple (Heichel & Turner 1976), balsam fir (Peine 1980), and Scots pine (Ericsson et al. 1985)), suggesting that some degree of compensatory growth may be a relatively common response of trees to defoliation.

Changes in the properties of regrowth foliage are not all beneficial to insect herbivores. Enhanced nitrogen and water status and an increase in the ratio of surface area to biomass (so that insects need to increase the area eaten to maintain an adequate intake of biomass) are likely to increase the susceptibility of compensatory growth to herbivory, while a reduction in sugar content may have an opposite effect. Valentine et al. (1983), for example, found that decreases in the sugar content of regrowth on black oak trees were correlated with decreases in the weight of gypsy moth pupae.

I also measured a transient increase in the tannin content of the regrowth foliage of the artificially defoliated trees (although no elevation of tannin content in dieback trees' foliage was evident).

In other studies similar increases in phenolic substances have been interpreted as part of an induced defence against subsequent herbivory (e.g. Haukioja & Niemela 1979; Wratten et al. 1984). While the tannin response I measured may well have been induced by damage (e.g. see Blake 1981), it failed to confer any effective resistance against insect herbivory.

Thus neither deterioration of the food resource (decreased soluble sugar) nor a possible induced chemical 'defence' (increased tannin) was sufficient to counter the increased susceptibility of both the artificially defoliated and the dieback trees to subsequent herbivory. Compensatory growth on both groups of trees incurred the cost of increased damage by insect grazers. This suggests that regrowth foliage on eucalypt trees may be at risk from resource regulation (sensu Craig et al. 1986) by their common insect herbivores, and this may be a crucial factor in the development of rural tree dieback.

Bryant et al.'s (1983) hypothesis of defence allocation during different phases of tree growth is apparently inappropriate to eucalypts and their insect herbivores. However, the hypothesis was developed in relation to herbivory by vertebrates. In addition to the transient change in tannin content of intermediate-form regrowth foliage reported here, juvenile-form epicormic foliage also tends to contain more tannin (Landsberg submitted c), and tannins may be more effective in defence against marsupial herbivores than insects (Landsberg submitted e; Freeland & Winter 1975; but see also Cork & Pahl 1984). Thus insects and vertebrates may have different sensitivities to defensive compounds in eucalypt foliage.

Increased insect herbivory on regrowth foliage is a surprisingly common feature of the response of many tree species to defoliation. In addition to this study it has been reported for birch trees in Sweden (Danell & Huss-Danell 1985), thorn trees in southern Africa (Webb & Moran 1978), calabash trees in Costa Rica (Rockwood 1974), and willows (Craig et al. 1986), several species of oaks (Auerbach & Simberloff 1984; Washburn & Cornell 1981), and red Alder trees (Williams & Myers 1984), in North America. For many of these studies the extent to which the increase in herbivory by insects is associated with a decrease in age of regrowth foliage, or with atypical times of

leaf production, or with changes in foliar properties associated with compensatory growth, is unclear. For the eucalypts I studied, differences between trees in the average age of their foliage accounted for some, but not all, of the variation in insect grazing. Since the trees all produced abundant new growth over the same period there were no major differences in patterns of leaf production. Thus at least some of the variation in insect grazing must have been in response to the physiological and morphological changes in foliage associated with compensatory growth.

Although enhanced susceptibility of foliage to herbivory following compensatory growth may seem maladaptive, the above examples suggest that it may also be rather common. It may be unavoidable whenever induced plant defences are ineffective in controlling populations of insects. Under these conditions the extent of enhancement of susceptibility will depend on a plant's capacity for compensatory growth, and is likely to be greatest for trees such as eucalypts, which have a very high potential to quickly replace lost foliage. Other tree species may have lower capacities for compensatory growth. For example, Valentine et al. (1983) found that, for the black oak trees they studied, the content of nitrogen as well as sugar declined in regrowth foliage, which was therefore unlikely to have had higher rates of photosynthesis than primary foliage.

Craig et al. (1986) hypothesized that the enhanced susceptibility of regrowth foliage of some tree species to herbivory may indicate that these species have adapted to stronger selective pressures than herbivory. This may well be true of eucalypts. High risk of fire is a feature of many Australian environments, and much of the endemic Australian flora shows adaptive traits which enables it to cope with fire (e.g. Gill et al. 1981). Thus rapid compensatory growth of many species of eucalypts may have evolved primarily in response to high fire risk, although at some cost in terms of enhanced susceptibility to insect herbivory.

Enhanced susceptibility does not inevitably result in damaging levels of herbivory on regrowth foliage. Weather conditions must also be favourable for insect growth and development, and the control exerted by predators and parasites on insect populations must be

relatively ineffective. (Although predators and parasites may exert a stronger controlling influence as foliar damage becomes more apparent; Heinrich & Collins 1983 and Faeth 1986.) Even when these conditions are met, the capacity for compensatory growth may be such that moderately high levels of herbivory may have little impact on tree growth. For example defoliation by Christmas beetles (Anoplognathus spp.) of up to 50% of the mature foliar area of young, plantation-grown eucalypts did not appear to reduce the rate of tree growth (Carne et al. 1974).

Thus although rapid compensatory growth of trees may enhance the susceptibility of regrowth foliage to insect herbivory, this need not necessarily be maladaptive, even in the absence of effective induced defences. However this strategy does pose a risk of herbivory becoming damaging whenever insect populations are limited mainly by their food, rather than by weather or predation, or when trees' capacity for compensatory growth is sufficiently reduced that recovery is no longer rapid enough to compensate for foliar loss.

This risk may become extreme for eucalypts growing on farms if management practices favour build up in insect populations, or reduce the growth potential of trees. Under these circumstances resource regulation by herbivorous insects may operate, and rural tree dieback may be accelerated.

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Table 1. Mean percentage of area removed from foliage samples from the groups of trees.

Sampling date	Unadjusted means:[1] H	DB	Def.	F(2,10)[4]	Significant model terms[2]	Adjusted means:[3] H	DB	Def.	F(2,10)[4]
7 Sep 83	8.4^{a}	13.9^{b}	9.1^{a}	2.09^{ns}	A,F	12.9^{a}	14.7^{a}	13.5^{a}	0.10^{ns}
14 Sep 83	"Def" trees artificially defoliated								
12 Nov 83	7.2^{a}	8.6^{a}	6.2^{a}	0.34^{ns}	A	13.4^{a}	17.0^{b}	16.4^{b}	2.21^{ns}
5 Jan 84	5.5^{a}	9.1^{b}	11.2^{b}	2.97^{*}	A,F,AxF	9.2^{a}	6.3^{a}	22.6^{b}	6.85^{**}
1 Mar 84	4.1^{a}	19.1^{b}	16.7^{b}	4.76^{**}	A,F	7.3^{a}	19.0^{b}	10.1^{ab}	1.80^{ns}
11 May 84	5.2^{a}	18.4^{b}	17.7^{b}	5.56^{**}	-	-			
3 Aug 84	10.9^{a}	20.6^{b}	35.2^{c}	6.57^{**}	-	-			
24 Sep 84	6.1^{a}	16.9^{b}	26.7^{c}	6.30^{**}	-	-			

[1] Calculated from mean values for each tree, not adjusted for any differences in leaf age or form. H = healthy trees, DB = dieback trees, Def = defoliated trees.

[2] Factors whose variation within each tree's sample significantly ($P<0.10$) contributed to variation among the trees. The factors tested were: leaf age (A), leaf form (F), their interaction (AxF), and their interaction with tree health (AxH and FxH). Dashes indicate that none of the factors was significant.

[3] Calculated by fitting a regression for each tree plus the model terms shown, so that means are adjusted to equalize the effects of the terms for the between-tree comparisons. Dashes indicate that adjusted means were equivalent to unadjusted means (no significant within-tree factors).

[4] F values calculated from ANOVA: *** $P<0.01$, ** $P<0.05$, * $P<0.10$, ns $P>0.10$. Means which have the same superscript were not significantly different on that date (t = difference between the means / standard error of the difference, $P<0.10$).

Table 2. Mean specific leaf weight (mg cm^{-2}) of foliage sampled from the groups of trees.

Sampling date	Unadjusted means: H	DB	Def.	F(2,10)	Significant model terms	Adjusted means: H	DB	Def.	F(1,10)
7 Sep 83	21.2^{a}	17.9^{b}	19.6^{ab}	3.24^{*}	-	-			
14 Sep 83			'Def' trees artificially defoliated						
12 Nov 83	16.6^{a}	12.6^{b}	8.4^{c}	22.74^{***}	A	24.3^{a}	22.0^{b}	21.9^{b}	13.10^{***}
5 Jan 84	15.0^{a}	11.7^{b}	10.4^{b}	9.39^{***}	A	20.7^{a}	17.2^{b}	16.7^{b}	6.95^{**}
1 Mar 84	17.5^{a}	$16\ 5^{ab}$	15.4^{b}	1.10^{ns}	A	18.0^{a}	17.2^{a}	16.2^{a}	0.83^{ns}
11 May 84	19.3^{a}	16.7^{b}	16.3^{b}	7.45^{**}	-	-			
3 Aug 84	20.5^{a}	17.9^{b}	18.6^{b}	3.19^{*}	-	-			
24 Sep 84	21.2^{a}	18.6^{b}	18.2^{b}	8.64^{***}	-	-			

(see Table 1 for explanation of headings)

Table 3. Mean nitrogen content (% dry weight) of foliage sampled from the groups of trees.

Sampling date	Unadjusted means: H	DB	Def.	F(2,10)	Significant model terms	Adjusted means: H	DB	Def.	F(2,10)
7 Sept 83	1.77^{a}	1.89^{a}	1.80^{a}	0.97^{ns}	-	-			
14 Sep 83			'Def' trees artificially defoliated						
12 Nov 83	2.18^{a}	2.44^{a}	3.77^{b}	17.56^{***}	A	1.16^{a}	1.24^{a}	2.22^{b}	10.93^{***}
5 Jan 84	1.75^{a}	1.88^{a}	2.27^{b}	7.18^{**}	-	-			
1 Mar 84	1.59^{a}	1.59^{a}	1.66^{a}	0.84^{ns}	A	1.58^{a}	1.57^{a}	1.65^{a}	0.51^{ns}
11 May 84	1.60^{a}	1.62^{a}	1.71^{a}	0.50^{ns}	-	-			
3 Aug 84	1.43^{a}	1.55^{a}	1.56^{a}	0.48^{ns}	-	-			
24 Sep 84	1.21^{a}	1.28^{a}	1.28^{a}	0.60^{ns}	-	-			

(see Table 1 for explanation of headings)

Table 4. Mean soluble sugar content (% dry weight) of foliage sampled from the groups of trees.

Sampling date	Unadjusted means: H	DB	Def.	F(2,10)	Significant model terms	Adjusted means: H	DB	Def.	F(2,10)
7 Sep 83	4.9^{a}	4.7^{a}	4.8^{a}	0.92^{ns}	-	-			
14 Sep 83			'Def' trees artificially defoliated						
12 Nov 83	4.6^{a}	4.1^{ab}	2.9^{b}	2.00^{ns}	-	-			
5 Jan 84	5.5^{a}	4.0^{b}	4.4^{b}	12.05^{***}	A	6.1^{a}	4.7^{b}	5.1^{b}	9.25^{***}
1 Mar 84	4.3^{a}	3.8^{a}	4.8^{a}	0.87^{ns}	A	3.7^{a}	3.3^{a}	4.1^{a}	0.40^{ns}

(see Table 1 for explanation of headings)

Table 5. Mean water content (% fresh weight) of foliage sampled from the groups of trees.

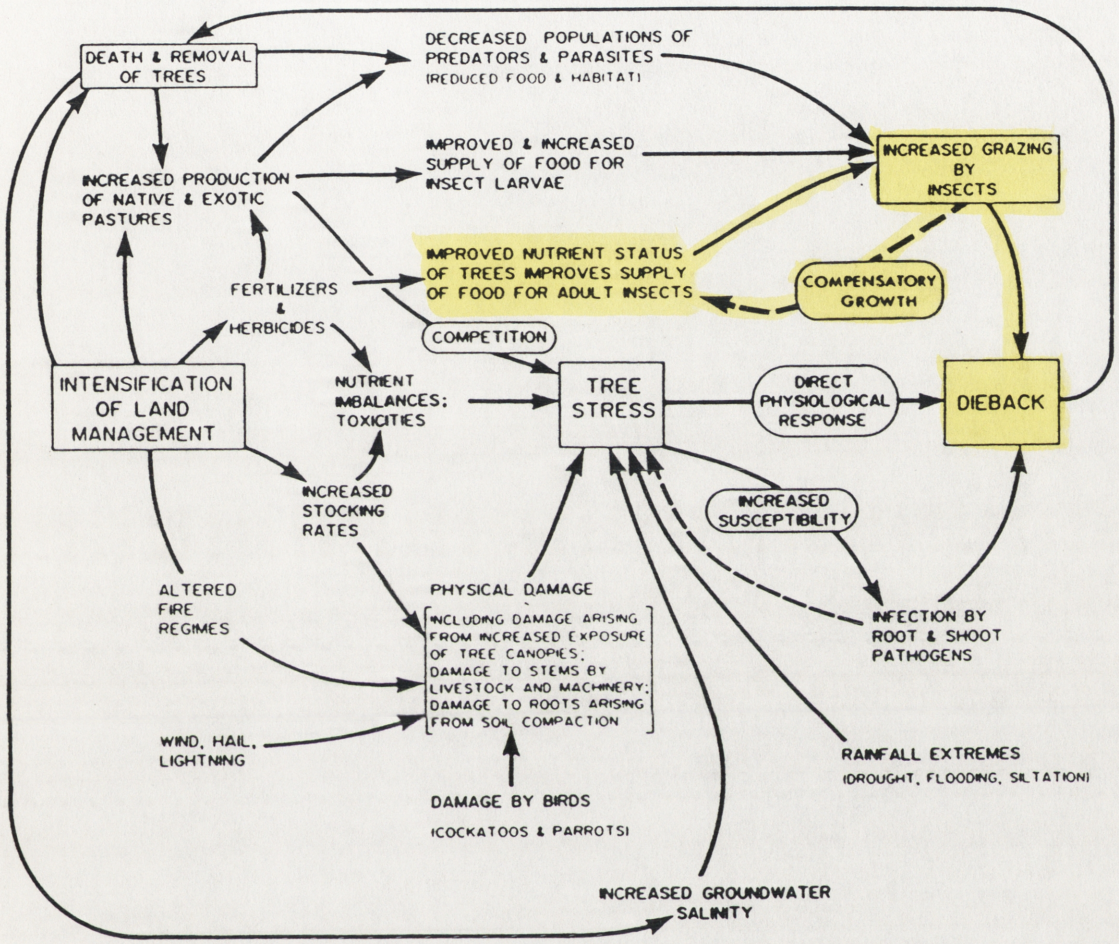
Sampling date	Unadjusted means: H	DB	Def.	F(2,10)	Significant model terms	Adjusted means: H	DB	Def.	F(2,10)
7 Sep 83	53.1^{a}	53.7^{a}	53.4^{a}	0.06^{ns}	A	51.9^{a}	49.8^{a}	50.9^{a}	1.81^{ns}
14 Sep 83			'Def' trees artificially defoliated						
12 Nov 83	60.2^{a}	63.8^{b}	73.4^{c}	29.33^{***}	A	47.7^{a}	48.4^{a}	51.3^{b}	3.73^{*}
5 Jan 84	61.2^{a}	64.1^{b}	66.7^{b}	3.47^{*}	A,AxF	30.9^{a}	51.7^{b}	33.5^{a}	7.41^{**}
1 Mar 84	57.6^{a}	55.1^{a}	57.7^{a}	0.82^{ns}	A	56.8^{a}	53.7^{b}	56.8^{ab}	1.33^{ns}
11 May 84	53.7^{a}	54.7^{a}	54.2^{a}	0.63^{ns}	-	-			
3 Aug 84	52.3^{a}	52.6^{a}	37.6^{b}	3.21^{*}	-	-			
24 Sep 84	49.9^{a}	50.9^{a}	51.2^{a}	1.05^{ns}	-	-			

(see Table 1 for explanation of headings)

Table 6. Mean tannin content (% dry weight of tannic acid equivalents) of foliage sampled from the groups of trees.

Sampling date	Unadjusted means: H	DB	Def.	F(2,10)	Significant model terms	Adjusted means: H	DB	Def.	F(2,10)
7 Sep 83	17.2^{a}	17.4^{a}	17.4^{a}	0.01^{ns}	-	-			
14 Sep 83			'Def' trees artificially defoliated						
12 Nov 83	17.6^{a}	17.9^{a}	24.8^{b}	5.91^{**}	A	24.4^{a}	24.6^{a}	27.3^{a}	0.36^{ns}
5 Jan 84	22.7^{a}	22.3^{a}	22.7^{a}	0.03^{ns}	A	13.4^{a}	11.8^{a}	11.9^{a}	0.44^{ns}
1 Mar 84	15.5^{a}	15.6^{a}	17.2^{a}	0.57^{ns}	A	14.1^{a}	13.3^{a}	14.9^{a}	0.78^{ns}
11 May 84	13.5^{a}	14.7^{a}	14.7^{a}	0.36	-	-			

(see Table 1 for explanation of headings)



Compensatory growth of eucalypts following defoliation increases the susceptibility of regrowth foliage to insect herbivory. Dieback may result when favourable foliar dietary quality is maintained by repeated cycles of insect defoliation.

INSECT HERBIVORY AND RURAL DIEBACK - AN OVERVIEW

The context of this study has been rural tree dieback, but its theme has been the interplay between variation in the dietary quality of trees' foliage and the susceptibility of the trees to defoliation by insects. The results have implications for both these aspects.

Of the dietary quality parameters I measured, the most reliable indicators of increased susceptibility to insect grazing were high concentrations of foliar nitrogen and low specific leaf weights. The importance of foliar nitrogen has often been demonstrated, but specific leaf weight has not been considered so frequently in herbivory studies. The amount of carbon assimilated by a plant is directly proportional to its leaf area. Insect grazing, too, is usually measured as a proportion of leaf area. However, plant productivity is usually measured by weight, and the consumption of leaf area by insects probably depends on the ratio of nutrient content to leaf biomass. With a knowledge of specific leaf weight, photosynthetic capacity and the relative nutritive value of plant tissues to insects can be better interpreted in terms of plant productivity and the extent of damage caused by the insects.

None of the chemical dietary quality parameters I measured appeared to be effective as defensive compounds; this was in contrast to relationships reported for many other insect/host plant systems, from which much of the classic theory of plant chemical defence was developed (e.g. Feeny 1970; Rhoades & Cates 1976). However, the results of my own and other recent studies (discussed in manuscript 3.1) suggest that this classic theory may not apply to all systems.

Despite the correlations between grazing damage and some aspects of foliar dietary quality, it proved very difficult to predict the susceptibility of foliage to grazing by insects from regressions of damage against dietary quality. This difficulty was partly the result of a high degree of intercorrelation between the quality variables and herbivory, and partly because of a high degree of variability in defoliation. Weather, predation and parasitism, insect life histories and habits, and chance, may all contribute to the pattern of grazing

by insects; some of these factors are probably also intercorrelated. Apparently, complexity of interactions is as much a feature of the relationships between plants and their herbivores as it is of other fields of ecological research.

The ways in which stress and defoliation influenced the dietary quality of E. blakelyi foliage illustrate this complexity. Environmental stress rendered foliage less favourable for insect herbivores, and severe defoliation rendered it more favourable: both of these responses are opposite to those reported from many other studies. I suspect that the difference between the response to stress that I measured and responses reported on other studies were more apparent than real, in that they probably reflect different types of stress response. The ways in which foliar properties are changed by stress depend very much on the severity and duration of the stress applied or described. When severe stress is allowed to develop rapidly in plant tissues (e.g. because severe environmental stress is applied suddenly), physiological changes such as osmotic adjustment may lead to the accumulation of soluble nitrogen compounds in the stressed tissues. Most physiological studies have been concerned with this kind of change in stressed tissues. However, if tissue stress develops more gradually (e.g. because more moderate environmental stress is applied over a longer time), adaptive changes at the level of the whole plant may mean that severe tissue stress is largely avoided. In these cases, changes in foliar chemistry may reflect the balance between reduced rate of uptake of nutrients and a reduced demand for them, rather than physiological responses to tissue stress. Further experiments are needed to establish whether physiological responses of plants to severe tissue stress, or adaptive changes to avoid it, are of more relevance to their insect herbivores. Such experiments should extend the range of severity and duration of the stresses applied, and should directly assess both plant and herbivore responses. Their major emphasis should be on field studies, since the expression of influences which seem important in isolation may be overwhelmed when other factors are free to operate.

I am puzzled by the difference between the defoliation response I measured (enhanced susceptibility) and that reported in other studies

(induced resistance). This is less likely to be a methodological problem, since the occurrence of eucalypt dieback strongly supports my contention that defoliated eucalypts do not produce effective defences against further herbivory. Apparently, eucalypts are not alone in this absence of response (manuscript 5.1). One of the tenets of the coevolutionary theory of insect/host plant relationships is that selection pressure exerted by herbivorous insects has enhanced the development of defence mechanisms in plants (Ehrlich & Raven 1964). The existence of systems in which insects are able to 'regulate' a favourable food resource through repeated cycles of defoliation of their host plant appears at odds with coevolutionary theory, in that resource regulation can only operate in the absence of effective defence mechanisms in host plants. Yet eucalypts appear to be very susceptible to resource regulation by their insect herbivores, at least when the insect populations are not controlled by other means. This may indicate that eucalypts have evolved in response to selective pressures very different from those influencing many other tree species. Alternatively, it may lend support to recent theses questioning some of the basic assumptions of insect/host plant coevolutionary theory. For example, Jermy (1984) analyzed the taxonomic relationships between herbivorous insects and between the plants on which they feed. From this he concluded that, for the majority of insect/host plant relationships, speciation of insects could not have caused speciation of host plants. Instead, he has proposed that the evolution of herbivorous insects has followed that of plants without major evolutionary feedback (sequential evolution, rather than coevolution). Thus Jermy suggests that the selection pressure exerted on plants by insect herbivory is generally weak or lacking, and could not have led to the development of defence mechanisms in plants. If this is generally true, then the apparent absence of effective defences in eucalypts becomes far less puzzling.

The mechanisms by which populations of eucalypt-defoliating insects are controlled are of very applied relevance, as indicated by the context of my study. What are the implications of my results in terms of understanding rural tree dieback? At least for insect-related dieback, a number of avenues for future research are indicated.

The cheapest means of increasing numbers of trees on farms is to encourage regeneration from mature trees already present. However, in regions where insect grazing pressure is severe, this strategy is associated with the risk that susceptibility to insect grazing may be hereditable. The extent to which foliar nutritional properties were determined by environment rather than by hereditary factors in my experiments is therefore very encouraging. It suggests that local provenances of trees may be no more at risk from dieback than other populations (although both may be equally at risk if their environment is not altered). Further research is needed to test whether this is more generally true.

Environmental stress may not be as important in triggering dieback as we had thought. However, this is a very tentative conclusion, based on preliminary studies of a single species of tree. Extensive testing of it is needed, again with an emphasis on field studies. In south eastern Queensland, dieback of river sheoaks (Casuarina cunninghamiana) on farms has been correlated with increasing streamwater salinity and with increasing levels of defoliation by a chrysomelid beetle (Johnston & Wylie 1984). This system could provide useful field data on interactions between stress, foliar quality, and herbivory.

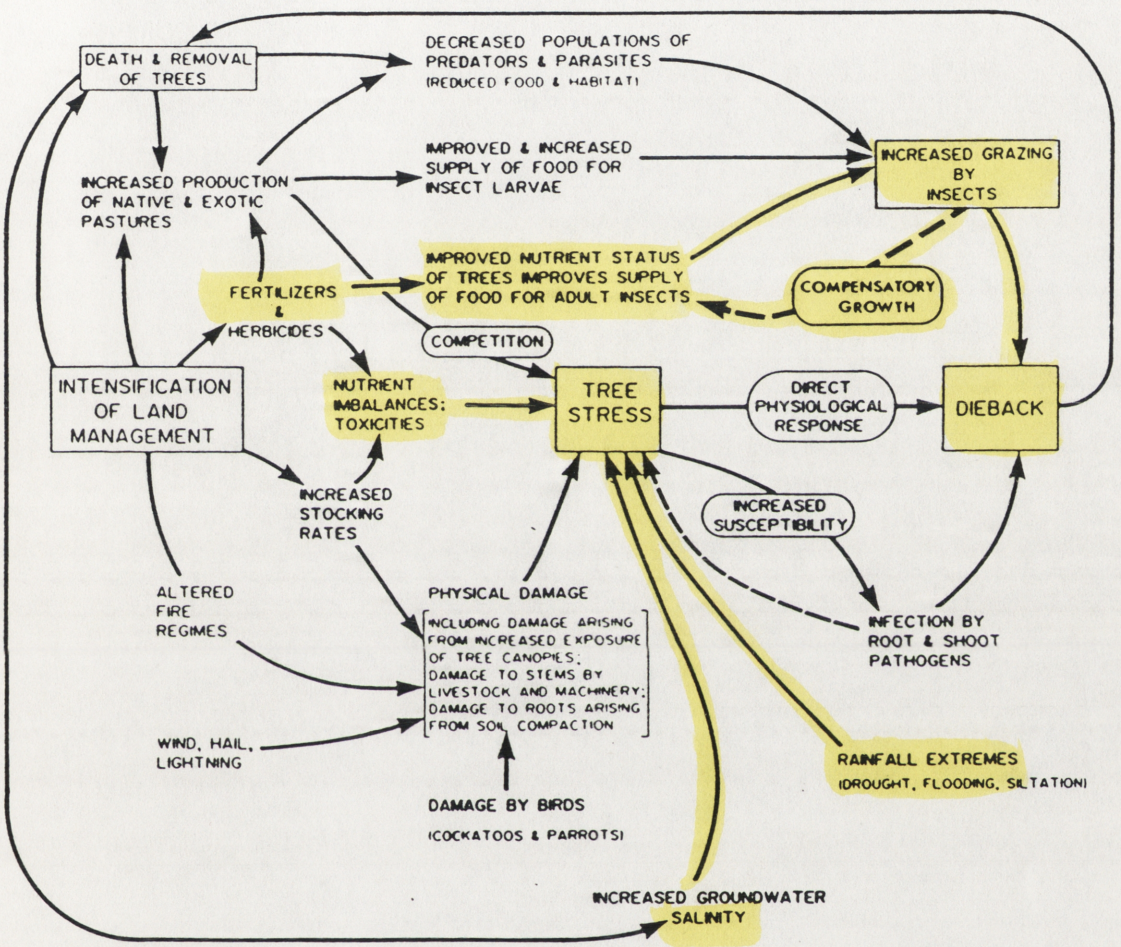
Nutrient enhancement of trees associated with management to improve pastures may be more important than environmental stress in triggering dieback. Manipulative field experiments, such as I attempted with seedlings, have the potential to provide elegant tests of hypotheses about the influence of both nutrient enhancement and stress on herbivory. Data about the properties of soils under dieback and healthy trees could also provide strong corroborative evidence. Despite the folklore about changing soil properties and rural tree dieback, I know of no comprehensive study of their relationship.

Dieback associated with cycles of severe defoliation alternating with periods of partial recovery may take many years to develop. This poses major problems in establishing how the dieback was initiated, because its maintenance, via the feedback of compensatory growth, may be largely independent of its initial cause. Compensatory growth in response to defoliation is probably typical of many species of

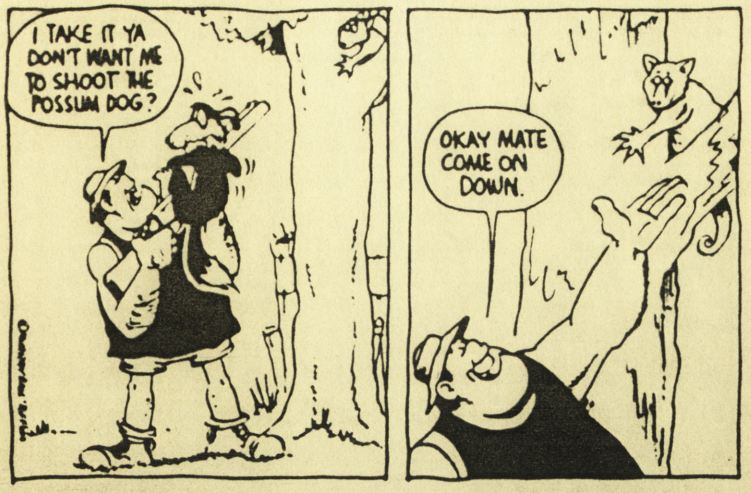
eucalypts, yet dieback associated with cycles of repeated defoliations is a major problem of trees on farms, rather than of trees in less-disturbed woodland or forest. This could be because the growth potential of trees on farms is reduced by environmental stress, such that they can no longer effectively replace lost leaf area. Alternatively, if the population of herbivorous insects on farm trees has increased, trees on farms could be suffering more defoliation by insects. Such an increase in the numbers of insects on trees could occur simply because of a reduction in the numbers of trees on farms, without a commensurate reduction in numbers of insects. It could also occur if farm management actually benefits herbivorous insects. Davidson (1980), for example, has suggested that the impoverishment of habitat on farms for the predators and parasites of leaf-feeding insects may be crucial in the development of rural tree dieback. These hypotheses are testable, and the development of effective measures for the longterm control of damaging populations of insects on farm trees depends on the outcome of such tests.

My study has been restricted to the interactions between dieback and defoliation by insects. Is rural tree dieback caused solely by insect damage? Preliminary experiments in New England with insecticides suggest that trees there can recover when insect populations are reduced (Mackay et al. 1984). Similar experiments have not been attempted in other regions, although they should be.

Most statements about the causes of rural dieback are at best testable hypotheses and, at worst, a combination of conjecture and folklore. Even the basic parameters of rural dieback have seldom been determined: the regions in which it occurs, the tree species that are affected, and their physical and biological environments are known for very few localities. Many of the factors on which dieback has been blamed (e.g. insect damage, fungal pathogens, herbicides, fertilizers, soil acidity, drought, soil compaction, damage by livestock) are not difficult to measure, but I am aware of very few studies that have attempted to do so. Until strategic research into rural tree dieback is encouraged and coordinated, conjecture and folklore will continue to be substituted for understanding of its causes and interactions.



The revised conceptual model of the development of rural dieback - more hypotheses than answers.



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Landsberg Jill (submitted d) The effect of stress on the nutritional quality of the foliage of seedlings of dieback-affected and healthy eucalypts. Submitted to Oecologia (Berl.)

Landsberg Jill (submitted e) Feeding preferences of common brushtail possums on seedlings of a woodland eucalypt. Submitted to Aust.Wildl.Res. .

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